Developmental Morphology of the Vegetative and Floral Shoots of Maize

By O. T. Bonnett

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O. T. Bonnett

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Developmental Morphology of the Vegetative and Floral Shoots of Maize

By O. T. Bonnett, Professor of Plant Genetics

THE EXTERNAL APPEARANCE OF MAIZE SHOOTS as they develop into the tassel and ear has been described in earlier publications (Bonnett, 1940, 1948). These descriptions pointed out definite stages in the development of the maize plant from germination to dehiscence of the anthers. Each stage can be identified from the external appearance of the shoots and the lateral organs that are developing from the parent shoot. However, nothing of the cytohistological characteristics of the main shoots or of the lateral organs (leaves and shoots) arising from them can be learned from whole, dissected specimens. Before the primordia of the lateral organs can be seen emerging from the shoots, cytohistological changes have occurred in the shoot apex and at the point of emergence of the primordia of the lateral organs. A knowledge of these events can only be gained by studying thin stained serial sections of the parts with a high-power microscope.

This publication illustrates and describes the cell arrangement in the apex of the shoots. It also describes the initiation of the primordia of the lateral organs of the shoots, the cell layers from which they arise, and the type of cell division which occurs at initiation of the primordia. Other publications on the cytohistological characteristics of the shoot and the lateral organs of grasses, including maize, have been limited to the vegetative stage. This study includes the tassel and ear and their parts. It is limited to a study of the shoots and the initiation and early stage of development of the primordia of the lateral organs.

REVIEW OF LITERATURE

An extensive literature on the morphology of grasses is available. These publications include the grasses that are of economic importance as well as others. Since this publication is concerned with maize, the literature reviewed is more or less limited to publications about the maize plant that have been helpful in this investigation.

Among the excellent publications dealing with the morphology and histology of grasses that of Arber (1934)[1] is the most extensive. It describes the general morphology and some of the developmental mor-

[1] See "Literature Cited," pages 45 to 47, for this and similar references.

phology of cereals, including maize, bamboo, and grass. Although Percival (1929) limited his study to the wheat plant, much regarding the morphological characteristics of grasses can be learned from this publication. In her excellent publication on plant anatomy, Esau (1953) included maize and other cereals. The morphological characteristics of grasses that are of taxonomic value are discussed in publications on the classification of grasses. Among many are Hackel (1890) and Hitchcock (1935).

There are many publications on the morphology, histology, and development of the maize plant. In a book "The Story of the Maize Plant," Weatherwax (1923) summarized some of his investigations, but the many publications from which material for this book was taken should also be consulted. The publication of Keisselbach (1949) has a large number of excellent drawings and photomicrographs illustrating various morphological details of the maize plant. Investigators working on the origin of maize, the characteristics of the maize ear, and the homology of the ear and tassel of maize have contributed a wealth of detail to maize morphology. Among others are the following publications: Collins (1919), Manglesdorf and Reeves (1939), Anderson (1944), Manglesdorf (1945), Anderson and Brown (1948), and Cutler and Cutler (1948). Some of the publications deal with specific parts of the plant: the development of the pistillate spikelet, Miller (1919); the developmental morphology of the caryopsis, Randolph (1936); the histology of the maize cob, Lenz (1948); and the epidermis of the leaf, Prat (1948).

External changes in the shoots of cereals and grasses during the development of the inflorescences and their parts have been investigated and reported by Bonnett (1935, 1936, 1937, 1938, 1940, 1948), Evans and Grover (1940), Fujita (1939), Noguchi (1929), Weber (1938, 1939), and others.

The cell organization within the shoot apex of grasses and other plants has been investigated by many workers. Foster (1939) summarized the work on the organization of the shoot apex and the various interpretations of the organization found. Stant (1952) discussed the zonation of the shoot of certain angiosperms. Popham (1951) reviewed the publications dealing with the basic organization of the vegetative shoot apex of vascular plants and classified the types.

Grass shoots have been studied by several investigators: maize by Abbe and Phinney (1951), and by Abbe, Phinney, and Baer (1951); oats by Kliem (1936) and by Hamilton (1948); bamboo by Hsü (1944); wheat by Rösler (1928); and maize and grass by Sharman (1942, 1945).

The vascular system of maize has been studied by Esau (1943), Laubengayer (1948, 1949), Reeves (1950), and Sharman (1942). It was not a part of this study.

MATERIALS AND METHODS

Several ear types were used in this study. They included four-rowed distichous and eight-rowed flints; dent types having 12 to 18 rows of kernels; and fasciated types with high row numbers and ramosa. When available, more than one variety of an ear type was studied. Inbred lines or uniform varieties were used to reduce variation among the specimens used. Different ear types were used in order to have a range of developmental patterns.

Most of the specimens were from field-grown plants. Greenhouse-grown plants were used when certain stages of development had not been obtained from field-grown plants. No essential difference was found in the developmental patterns of plants grown in these two ways.

Plants were sampled at progressive stages in their development. The developmental stages ranged from seedlings 72 hours old to plants with completely differentiated flowers.

Whole plants, dissected shoots, and plant parts were killed and fixed in a solution of formalin, acetic acid, and alcohol, and also in Craf. The tertiary butyl alcohol method described by Johansen (1940) was used to dehydrate, infiltrate, and embed material for sectioning. Most of the staining was done by Foster's (1934) tannic acid — iron chloride — safranin method. Sharman's (1943) tannic acid — iron alum — safranin — Orange G procedure was also used. The staining procedure of Popham, Johnson, and Chan (1948) also gave excellent results.

Whole mounts were also made of killed and fixed material. The specimen was placed in cold lactic acid for a few days to permit the acid to penetrate the plant tissue. A glass beaker containing the specimen in the lactic acid was then immersed in boiling water until the specimen was clear (5 to 10 minutes). The excess lactic acid was poured off and the material soaked in several changes of distilled water to remove the lactic acid. The cleared specimens were stained in two ways. They were transferred from water to tannic acid and left for 1 to 2 minutes, then transferred to iron chloride, rinsed in distilled water, dehydrated with an alcohol series through xylene, and mounted in balsam. The other sequence used was to dehydrate through an alcohol series to 95 percent alcohol, stain with Bismark brown Y and fast green

FCF (Morley, 1949), dehydrate with an alcohol series through xylene, and mount in balsam.

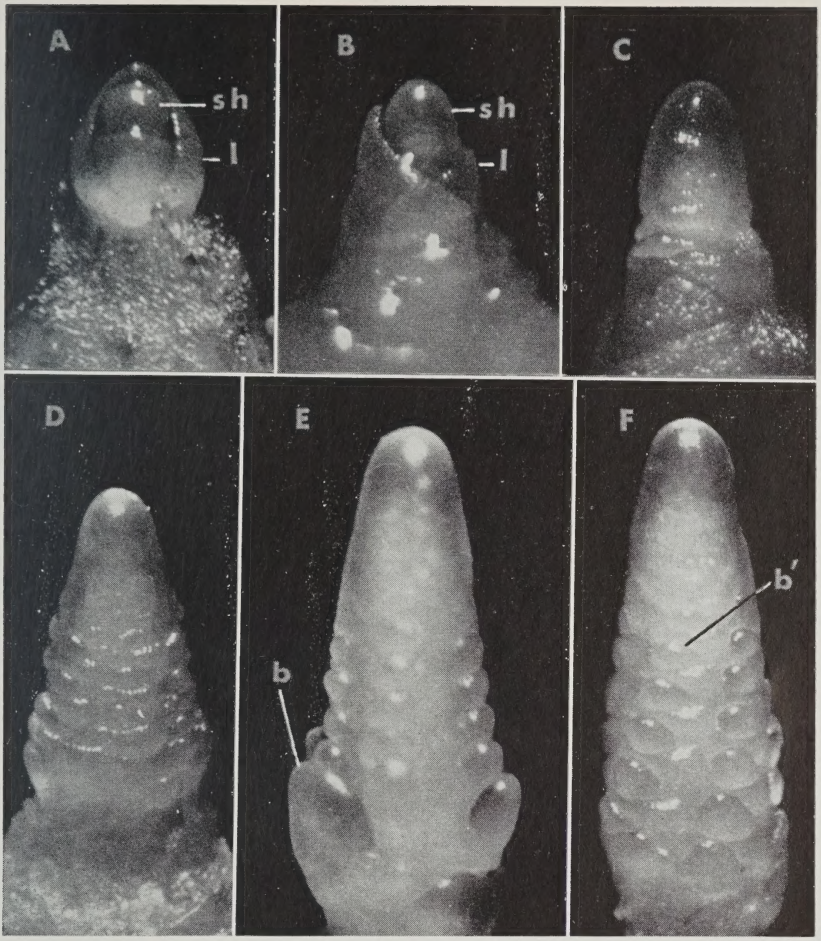
MORPHOLOGICAL DEVELOPMENT: EXTERNAL APPEARANCE

From germination to the dehiscence of the anthers, the shoot of the corn plant passes through three stages of development: the vegetative, the transitional, and the reproductive. In the vegetative stage the shoot apex remains short, there is no internode elongation, and leaf primordia arise acropetally in alternate succession at a certain distance from the shoot apex (*Fig. 1: A, B*). Axillary shoots are produced and leaves arise from their apexes in the same order as those of the main axis. The transitional stage is of short duration and consists of an elongation of the shoot apex (*Fig. 1: C*). The reproductive stage begins with the initiation of branch primordia at the base of the elongated transitional-shoot apex. In this stage the internodes of the stem elongate and the branches, spikelets, flowers, and their parts differentiate and develop.

Branch primordia and subtending ridges are the first parts of the inflorescence to appear upon the surface of the elongated transitional-shoot apex. In the tassel the branch primordia are of two kinds: those at the base of the tassel, which elongate to become the long branches; and the spikelet-forming branches on the central axis and on the long branches of the tassel. The branch primordia of the ear, except for ramosa, are spikelet-forming branches. A ridge subtends each branch primordium of the tassel and ear (*Fig. 1: D, E, F*). The ridges subtending the lateral shoots in the tassels are more prominent in some maize types than in others. In all types of maize that have been studied, the ridges subtending the spikelet-forming branches are more prominent in the ear than in the tassel.

In both the tassel and the ear, the spikelet-forming branches divide into two unequal parts to produce the spikelet initials (*Fig. 2: A, B, C*). In the tassel the spikelet developing from the larger division becomes the pedicellate spikelet and that from the smaller division the sessile spikelet (*Fig. 2: B-si′ and si*) but in the ear this distinction is not apparent (*Fig. 3: A, B*). The pedicellate spikelet is always ahead of the sessile spikelet in development.

Two flowers are produced in each spikelet. In the tassel both flowers are functional, each containing three anthers and an aborted pistil. In most maize types only the upper flower of the spikelet of the ear develops; the lower flower aborts. Pistils form in the functional



External appearance of shoots of maize in the vegetative, transitional, and floral stages. **(Fig. 1)**

A. Main shoot in the vegetative stage, four leaves visible. Leaf primordia partly enclose the shoot apex. ×50.

B. Main shoot in the vegetative stage viewed at right angles to the plane of the leaves. ×50. (Photo by E. R. Leng, University of Illinois)

C. Main shoot in the transition stage, elongating, preceding the initiation of branch primordia. ×40. (Photo by E. R. Leng, University of Illinois)

D. Ear shoot, showing spikelet-forming branches as protuberances, subtended by ridges. ×55.

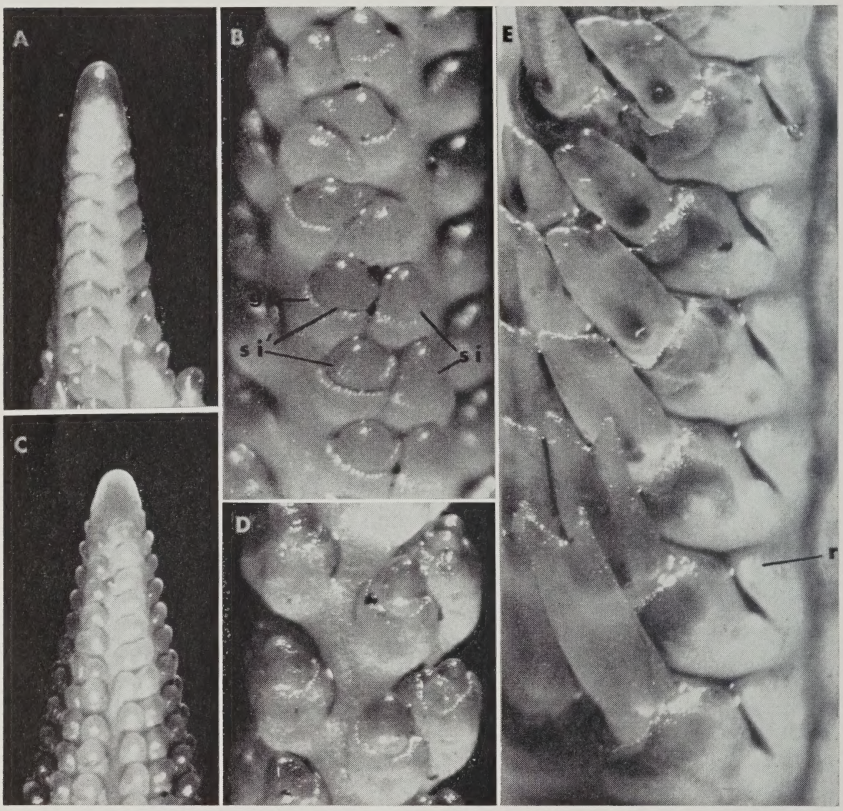
E. Early stage in the development of the tassel showing long branch primordia at the base and spikelet-forming branches toward the apex. ×50.

F. Ear shoot more advanced than in D. Spikelet-forming branches and the subtending ridges are shown and the beginning of the rachis-flap between the rows of spikelet-forming branches. ×55.

(b = long branch; b′ = spikelet-forming branch; l = leaf primordium; sh = shoot apex)

flowers of the ear, but the stamens abort. Thus the tassel functions as a staminate and the ear as a pistillate inflorescence.

The empty glumes are the first parts of the spikelet to differentiate (*Fig. 2: B-g* and *Fig. 3: A-g*). They conceal the earliest stages of flower development. Sectioned material, illustrated and described later,



Various stages in the development of the shoot apex and spikelets. (Fig. 2)

A. A portion of the central axis of a tassel. Some of the spikelet-forming branches are dividing to produce two spikelet primordia. Acropetal development is shown. ×27.

B. Section of the central axis of the tassel showing spikelet-forming branch primordia and spikelet primordia. ×55.

C. Tip of an ear. ×20.

D. Section of a tassel having spikelets at an advanced stage of development. Glumes partly enclose the flowers. The pedicellate and sessile spikelets can be identified. ×40.

E. Section of an ear. Silks have biparted tips. Rachis-flaps well developed. ×27. (g = glume; r = rachis-flap; si' = pedicellate spikelet; si = sessile spikelet)

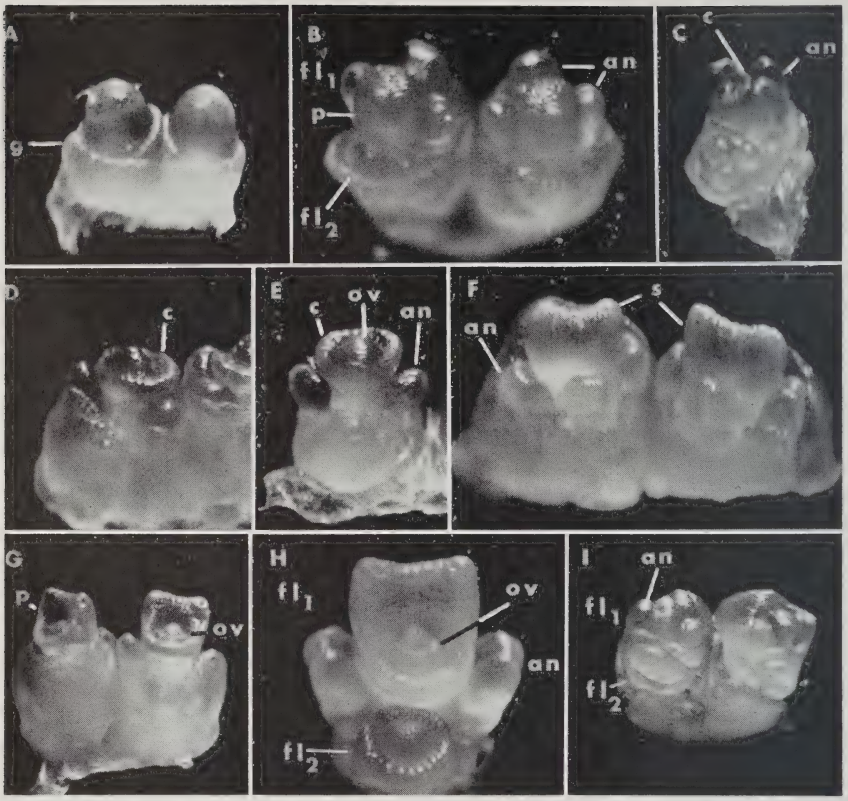
shows the details of the initiation of the primordia of the flower parts and the sequence of their development.

Although the stamens of the pistillate flowers abort, their position in the flower and their early stage of development are the same as in the flowers of the tassel. This is evident when the spikelets shown in *Fig. 3: C-an and I-an,* which are from a tassel, are compared with flowers from an ear, shown in *Fig. 3: B-an.* The carpels appear as a ridge upon the shoot apex of the flower (*Fig. 3: C-c, D-c, and E-c*) resembling the early stage of leaf development. The margin of the carpel primordia grows more rapidly on one side than on the other (*Fig. 3: D-c and E-c*). Soon two distinct points appear (*Fig. 3: F-s, G, and H*) which become the two members of the biparted tip of the mature silk. The ovule differentiates from the shoot apex of the flower (*Fig. 3: G-ov and H-ov*). The opening above the ovule becomes smaller, but it is never completely closed, remaining as the stylar canal. *Figure 3: H* shows a spikelet of Country Gentleman sweet corn, a type in which both the upper and lower flowers are functional. However, when both flowers of a spikelet in the ear develop, the upper flower develops more rapidly than the lower flower.

MORPHOLOGICAL DEVELOPMENT: CYTOHISTOLOGICAL CHARACTERISTICS

Much of value can be learned from a study of the external changes in the morphology of a shoot apex of maize as it passes through the various stages of its development. However, to learn something of the cytohistological characteristics of the developing shoot apex and the cytohistology of initiation and development of the primordia of the plant parts, serial sections of plants and plant parts must be studied at different stages of their development.

So far as these studies indicate, the lateral organs arising from the shoot of the corn plant can be placed in two groups, depending on their point of origin in the cell layers that make up the shoot apex. In the first group are the foliage leaves, prophylls, glumes, lemmas, paleas, carpels, and integuments whose primordia are initiated by periclinal divisions in the first and second cell layers of the shoot apex. In the second group are shoot and shootlike parts, the tillers, spikelet-forming branches, spikelets, floral branches, stamen, and lodicules. The shoots and shootlike parts are initiated by periclinal divisions in cells located in the third cell layer of the shoot apex. The position, number, and behavior of the initiating cells are different for each of



Development of spikelets. **(Fig. 3)**

A. A pair of pistillate spikelets. As indicated by glume development the lateral spikelet (right) is not as far advanced as its mate. ×55.

B. Pistillate spikelets of Country Gentleman sweet corn. Both flowers of the spikelet are functional, but the upper flower develops more rapidly. Stamen primordia are initiated in pistillate spikelets. ×55.

C. Flowers of a spikelet from a tassel, glumes removed. The upper flower is the most advanced. Both flowers develop functional stamens. The pistil is initiated but aborts. ×38.

D. Early stage in the development of the carpel of a pistillate spikelet. At this stage the carpel primordium resembles a leaf primordium. ×40.

E. Another view of a carpel primordium of a pistillate spikelet, glumes removed. Note the rudimentary stamen and the ovule, which is partly enclosed by the carpel primordium. ×55.

F. An adaxial view of a pair of pistillate spikelets. The biparted tip of the style is beginning to develop. ×55.

G. Adaxial view of two spikelets. The ovule can be seen in the opening that partly closes forming the stylar canal. ×40.

(*Continued on next page*)

the two groups of parts. There are also differences in the developmental patterns of the two groups of plant parts.

Organization of the Shoot Apex

The shoot apex of *Zea mays* has been classified by Popham (1951) as Type VII, the usual angiosperm type. A diagrammatic drawing of this is shown in *Fig. 4*.

In this type there are four zones (Popham, 1951). The first zone is the mantle (M) (tunica) consisting in maize of a single layer of cells in which the cells divide anticlinally (at right angles) to the surface of the shoot. However, periclinal cell divisions (cell division parallel to the surface of the shoot) occur in the initiation of foliage leaf primordia and prophylls and also in the shoot apex of flowers when the primordia of the leaflike parts are initiated. Zones 2, 3, and 4 are in the shoot apex beneath the mantle, in the area which has been designated as the corpus. Zone 2 (SA), the subapical initials, are a self-perpetuating group of irregularly shaped cells that may divide in any plane. They contribute to Zone 3 (CM), the central meristem, and to Zone 4(P), the peripheral meristem. The cells of Zone 2 may be larger than those of the other zones and they have distinct vacuoles. This zone is added to by periclinal cell divisions in the second cell layer at the apex of the shoot. Zone 3, the central meristem, lies directly below Zone 2. This zone is added to by periclinal cell divisions of the cells of Zone 2 bordering on Zone 3. Within Zone 3 cell division is mostly at right angles to the long axis of the shoot, thereby producing long files of cells, rib meristem, which form the pith cells. Provascular strands also develop in this area. Zone 4, the peripheral meristem, forms a cylinder beneath Zone 2 and surrounding Zone 3. The cells of this area are small deeply staining cells and apparently have no vacuoles or only small ones. This is the zone in which the spikelet-forming branch primordia are initiated and in which the vascular system supplying the spikelets develops.

(*Fig. 3, continued*)

H. Pistillate spikelet, glumes removed, of Country Gentleman sweet corn. Both flowers develop functional pistils, but the upper flower is much more advanced in its development. The carpel is developing on the pistil of the lower flower. In the upper flower the well-formed stamens abort. The outer integument can be seen as a ridge around the ovule. ×65.

I. Staminate spikelets. Both flowers of a spikelet develop functional stamens. ×40.

(an = anther; c = carpel; fl_1 = upper flower; fl_2 = lower flower; g = glume; ov = ovule; p = pistil; s = silk)

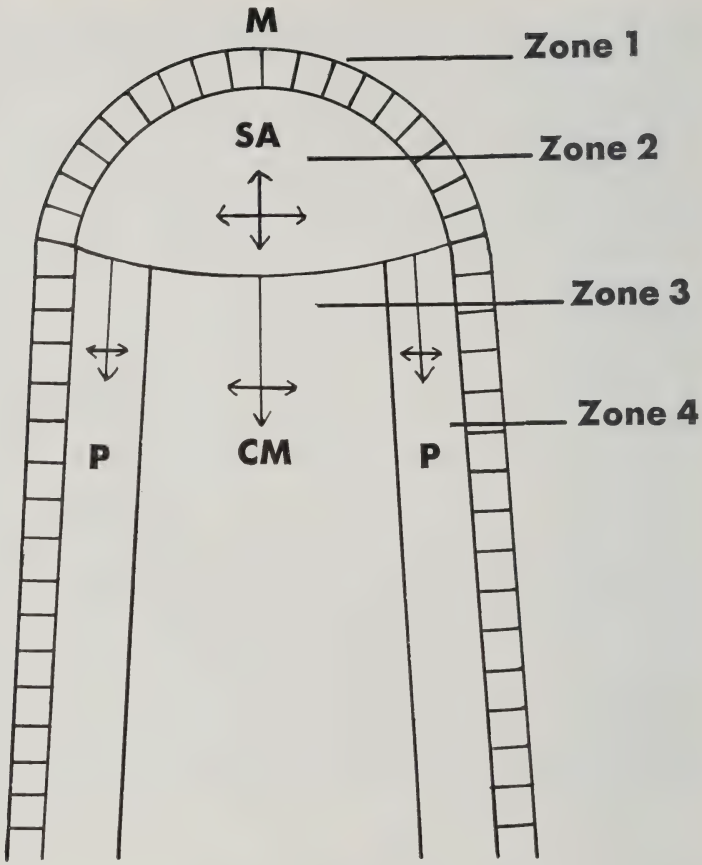


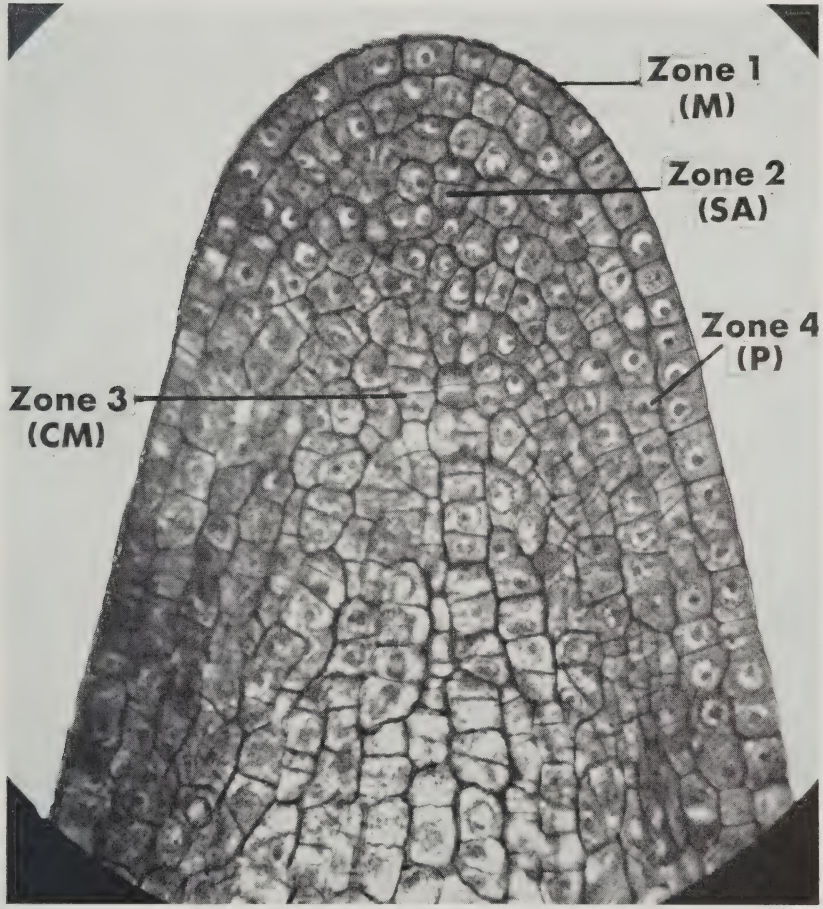
Diagram of a shoot apex of the usual angiosperm type, Type VII, to which maize belongs, as shown by Popham (1951). **(Fig. 4)**

Zone 1, M, mantle of a single cell layer; cells divide anticlinally. Zone 2, SA, subapical initials, a self-perpetuating group. Zone 3, CM, central meristem, the region where rib meristem is formed, later the pith. Zone 4, P, peripheral meristem forms a cylinder around Zone 3. In this region the spikelet-forming branches are initiated.

The different zones of the shoot apex of maize are shown in *Fig. 5*, a photomicrograph of a median longitudinal section of a well-developed tassel of a polyploid plant of maize.

Each of the meristematic zones illustrated diagrammatically in *Fig. 4* is shown. The mantle (M), consisting of a single cell layer, the subapical meristem (SA), and the central meristem (CM), can be easily identified. The peripheral meristem (P) merges with the central

meristem so that there is no clear line of demarcation. The peripheral meristem at the right of the illustration is three cells wide. It can be identified by the anticlinal and periclinal cell divisions in it. In the central meristem the cell divisions are at right angles to the long axis of the shoot. Groups of cells characteristic of rib meristem can be seen in the central meristem. Where the subapical meristem borders the meristematic zones beneath it, cell divisions that contribute to the maintenance of these zones can be found.



Photomicrograph of the shoot apex of the main axis of a polyploid plant of maize. The meristematic zones that are shown in Fig. 4 can be identified. ×450. (Fig. 5)

The Vegetative Shoot

Not all the meristematic zones are clearly defined in the shoot apex of the tassel or ear of the maize plant in the early stages of development. As the shoot becomes older, the meristematic zones become more clearly defined, and they are fully developed in the floral shoot (*Fig. 5*). The lateral shoots, tillers, spikelets, and flowers show the same progressive development of meristematic zones as the main shoot, except that the peripheral meristem is not as prominent in the shoots of spikelets and flowers. The following descriptions of the apex of the main shoots at successively more advanced stages of development will illustrate the progressive development of meristematic zones.

A median longitudinal section of a shoot of a seedling of the Illinois High Oil strain of maize is shown in *Fig. 6: A*. This seedling was sampled about 72 hours after germination began. The cells are large and contain large nuclei. The large cells and nuclei are probably an indication of preparation for division following the resting stage of the embryo of the mature seed. The mantle consists of one layer of cells with the cell walls at right angles to the surface of the shoot. There is no clear indication of definite zones in the shoot apex beneath the mantle. There is a slight bulge on the right side of the shoot apex at the point of origin of the next leaf primordium. There seems to be a single apical cell, although there was no evidence of such a cell in other specimens.

A shoot of a seedling of American Long Kernel (fasciated type) with one leaf visible is shown in *Fig. 6: C*. The four zones are not yet clearly defined. The group of subapical cells can be seen beneath the

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Median longitudinal sections through the main shoot of maize plants at various stages of development. (Fig. 6)

A. Shoot of a seedling of the Illinois High Oil strain after 72 hours of germination. ×350.

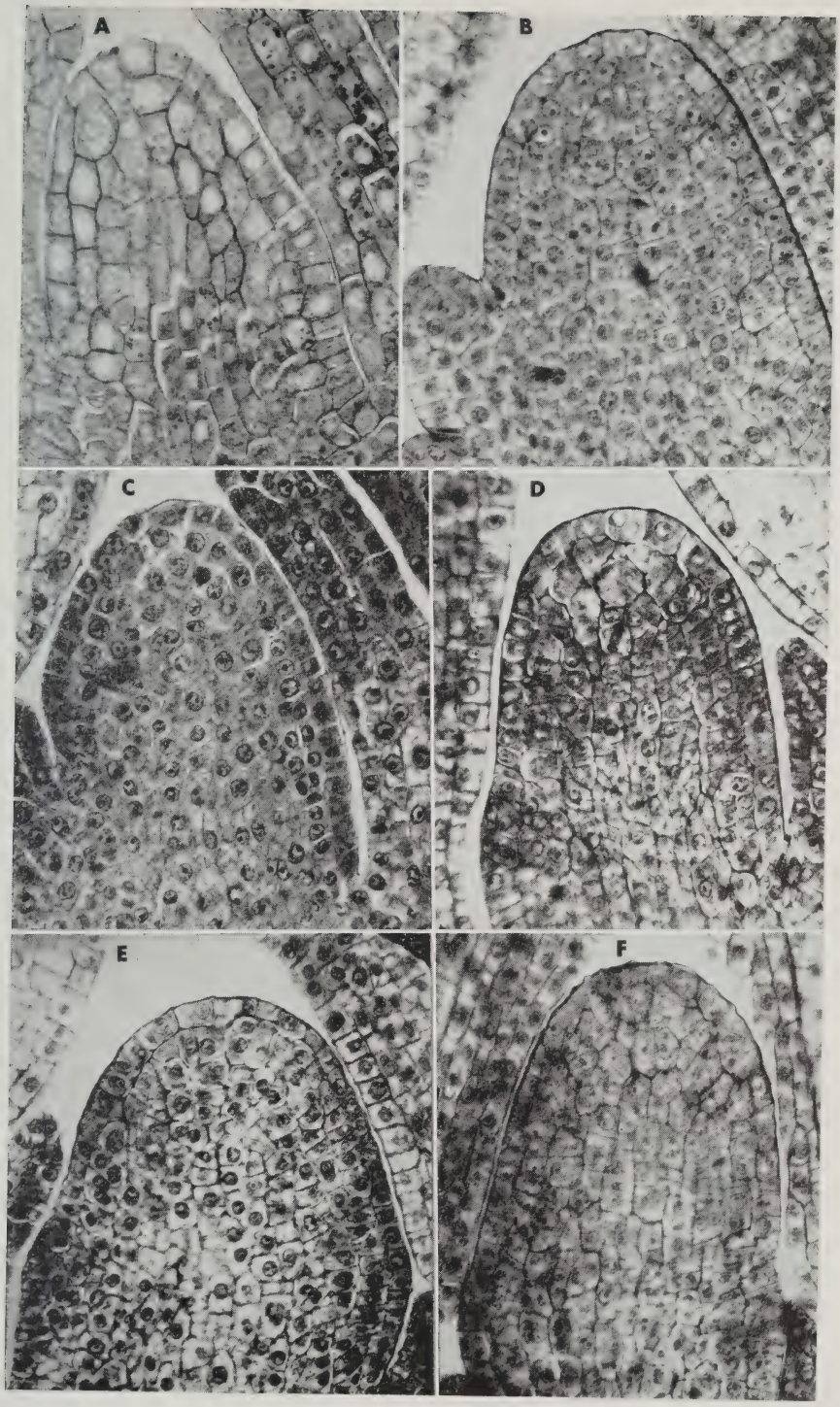
B. From a seedling of the Illinois High Protein strain having four leaves visible. ×300.

C. Shoot of American Long Kernel (fasciated type) seedling having one leaf visible. No evidence of fasciation is shown at this stage of development. ×300.

D. A section through the shoot of a 4-row (distichous type) having four leaves visible. The shoot is in the early part of the transitional stage, elongation has begun. A leaf primordium is developing on the left side of the shoot at the base. ×300.

E. Japanese Hull-less popcorn. This type has a short ear with a high number of rows of kernels. The shoot apex is broad with a large number of subapical initials as contrasted with the narrow apex of the 4-row type in D and Longfellow flint, an 8-rowed type, in F. ×300.

F. Longfellow flint, an 8-rowed type. The shoot is in the transition stage. ×300.



(Fig. 6. — See opposite page)

mantle at the apex of the shoot, but the peripheral and central meristems are not yet defined. At the right of the photomicrograph, periclinal divisions in the second cell layer indicate the initiation of the next leaf primordium. A shoot apex of a seedling of the Illinois High Protein strain of maize with four leaves visible is shown in *Fig. 6: B.* This shoot is more advanced in its development, and the presence of the four meristematic zones is shown. Older shoots are illustrated in *Fig. 6: D, E, and F.* All the meristematic zones can be seen in these shoots.

The number of cells in the subapical meristem varies with the diameter of the shoot. Types of maize with a low number of rows of kernels in the ear tend to have a shoot with a smaller diameter than those types with many rows. The difference in the number of cells in the subapical meristem can be seen by comparing *Fig. 6: D,* a shoot of a 4-row (distichous) flint type, with *Fig. 6: E,* a shoot of Japanese Hull-less popcorn, which has a very short, blunt ear with a high number of rows of kernels. The shape of the subapical meristem is different in maize types having 16 rows of kernels or fewer from that of a type having a high row number, a fasciated type. In the types having 16 or fewer rows, the subapical meristem is spherical while in certain fasciated types the subapical meristem consists of a narrow band, a few cells deep, extending across the shoot apex beneath the mantle layer. Japanese Hull-less is a fasciated type, but it does not show the narrow band of subapical meristem that is found in some fasciated types.

Transition Stage

The transition stage is a definite stage in the development of the shoot of both the ear and tassel. In this stage the shoot apex elongates in preparation for the initiation of the long branches of the tassel and the spikelet-forming branches of tassel and ear. The transition stage is illustrated in *Fig. 1: C* and *Fig. 6: D and F.* No foliage-leaf primordia are produced. The four meristematic zones become more clearly defined (*Fig. 6: F*). Zone 1, the mantle, consists of a single layer of anticlinally dividing cells. In Zone 2, the subapical meristem, the cells are fairly large and have vacuoles. Long files of four or more cells, the rib meristem, are shown at some distance, basipetally, from the margin of the subapical meristem, while just beneath the subapical meristem the cells are in pairs. The peripheral meristem, Zone 4, is one to three cells wide. Just beneath the margin of the subapical meristem, Zone 4 is only one cell wide but it is two cells wide toward the base of the shoot.

The period of time covered by the transition stage varies with growing conditions, the type, and the variety. Leng (1951) used the number of visible leaves as a guide in determining the stage of development of the shoot of maize growing in the field. In the Illinois High Oil strain of maize, elongation began when the seventh leaf could be seen in the whorl of the sixth leaf, and by the time that the eighth leaf was fully developed, branch primordia could be seen at the base of the shoot apex. This covered a period of about three days.

Size of the Shoot

No exact figure can be given for the diameter of the shoot apex of the main axis of the maize plant. This varies with the age of the plant and the ear type and among plants of the same variety or ear type. During the vegetative stage of development, before the shoot begins to elongate, it is approximately as long as it is wide. At the end of the transition stage, the shoot is about twice as long as it is wide. After floral initiation the shoot continues to increase more in length than in diameter until the tassel or ear is fully matured.

Some measurements of the diameter and length of the main shoot just above the insertion of the last leaf primordium were made. The plastochron stage of the specimens measured was not determined. The median longitudinal section of a seedling of the Illinois High Oil strain after 72 hours germination at approximately 70° F. was 106 microns long by 108 microns wide. Seedlings with one leaf visible ranged from 103 microns in diameter for 4-row (distichous) to 146 microns for the Illinois High Protein strain. Longfellow flint and a fasciated type were within this range. There is a gradual increase in the diameter of the shoot apex as the plant develops. At a stage when four leaves were visible, some measurements of the diameter of the shoot apex varied from 129 microns for 4-row to 270 microns for Japanese Hull-less popcorn. These measurements are only approximations since there is variation among plants of a given variety as well as among different maize types.

The Foliage Leaf

The cell layers involved and the type of cell division that takes place in the initiation of the foliage-leaf primordium of cereals and other grasses have been described by other authors. Detailed descriptions of leaf initiation in cereals and grass have been published by Rösler (1928), Kliem (1936), and Sharman (1942, 1945), each of whom cites earlier work on this subject. Less detailed accounts have

been given by Arber (1934), Hsü (1944), Hamilton (1948), and Abbe, Phinney, and Baer (1951).

Foliage leaves of the corn plant are in two ranks (distichous), one at each node on opposite sides of the stem (alternate). The first foliage leaf is opposite to the scutellum (Randolph, 1936, and Arber, 1934). The next leaf arises on the opposite, the scutellar, side of the stem above the insertion of the first foliage leaf. In a study of fourteen inbred lines of corn, Hubbard (1951) found no fewer than four or more than five foliage leaves. They ranged from the first foliage leaf large enough to enclose the shoot to a primordium consisting of a ridge partly encircling the shoot apex. The foliage leaves and the shoot apex are enclosed by the coleoptile.

Foliage-leaf primordia are initiated by periclinal cell divisions in the first and second layers of the cells of the shoot apex (*Fig. 7: A*). The first periclinal division may occur either in the first cell layer or in the second cell layer. In *Fig. 6: A*, opposite the slight bulge in the contour of the shoot apex, there are indications that a periclinal division has occurred in the second cell layer. In other cases periclinal cell divisions are found in the first cell layer. Several periclinal cell divisions are usually found at the point of the initiation of the leaf primordium. They may be the result of the simultaneous division or of a closely timed sequence. Kliem (1936) classified the leaf primordia of oats into three types, A, B, and C, depending on whether the number of cells dividing periclinally in the initiation of the leaf primordium was one, two, or three. Such a classification is probably not justified because the number of cells involved may vary in the same primordium, depending on the point at which the section is made (*Fig. 7: B, C, D, E*).

Leaves form acropetally and at a point opposite the insertion of the preceding leaf. Leaves and other parts always develop a certain distance back from the apex of the shoot. The apex of the shoot is an area of rapidly dividing cells where the various meristematic areas are

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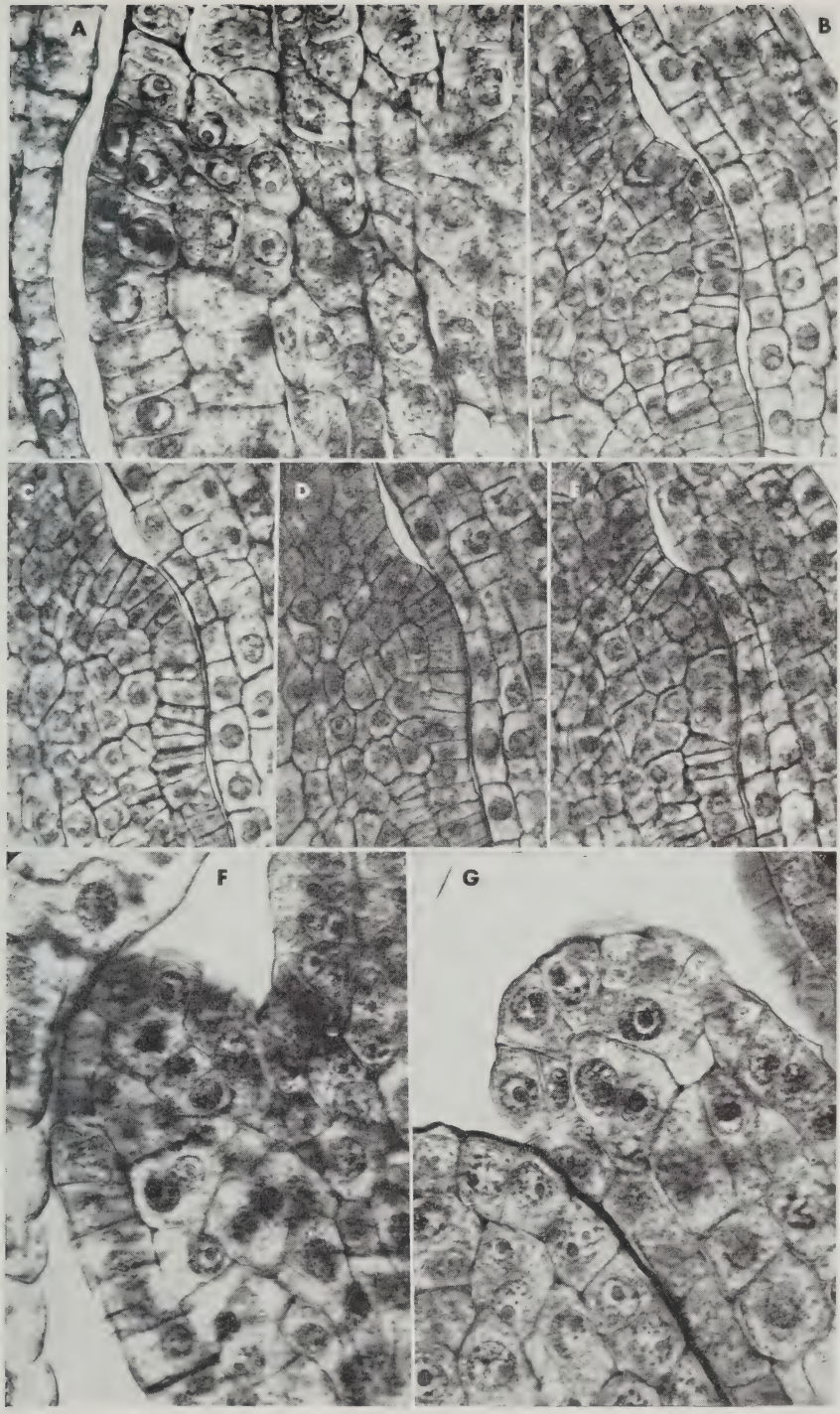
Longitudinal sections through leaf primordia at different stages of initiation and development. (Fig. 7)

A. A longitudinal section through a leaf primordium at the beginning of its initiation. Periclinal cell divisions have occurred in the first and second cell layers of the shoot. ×730.

B-E. Successive longitudinal sections 10 microns thick through the same leaf primordium. Different cell division patterns are shown in each section. Periclinal cell divisions have also occurred in the cell layers beneath the first and second cell layers. ×440.

F, G. Longitudinal sections through the tip of leaf primordia to show periclinal divisions at the margin of the leaf. ×730.

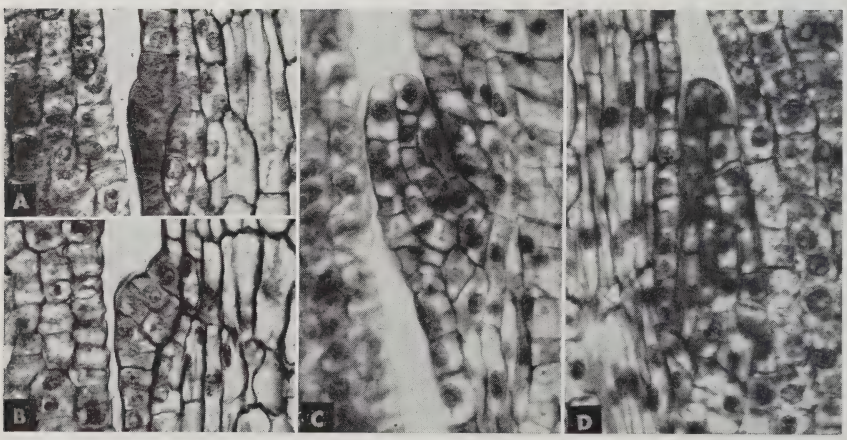


(Fig. 7. — See opposite page)

being maintained. It appears that a certain size must be attained by the shoot apex before the differentiation of parts begins (Abbe and Phinney, 1951).

From the point of the initiation of the foliage-leaf primordium, periclinal cell divisions proceed laterally around both sides of the shoot apex until the margins nearly meet (Sharman, 1942). Rapid cell divisions in this area produce a collarlike swelling (*Fig. 1: A, B,* and *Fig. 7: B, C, D, E*) on the surface of the axis. Growth is more rapid at the point of initiation of the leaf primordium and on the abaxial side of the primordium. This growth results first in a fold of tissue (*Fig. 7: F*) and finally the growth encloses the shoot apex (*Fig. 1: A, B*). For a time meristematic cells in the second cell layer at the tip and along the margins of the leaf (*Fig. 7: G*) provide for growth in length and width. Anticlinal divisions in the surface layer keep pace with the increase in the size of the leaf.

The ligule. The ligule is a thin membranous structure that develops on the inner surface of the leaf at the junction of the leaf sheath and the blade. It fits closely against the stem of the plant and serves to prevent the entrance of foreign objects between the stem of the plant and the leaf sheath. A group of three or four meristematic cells is found in the epidermal layer at the point where the leaf sheath and blade are joined (Sharman, 1941, 1942). The ligule is initiated by a

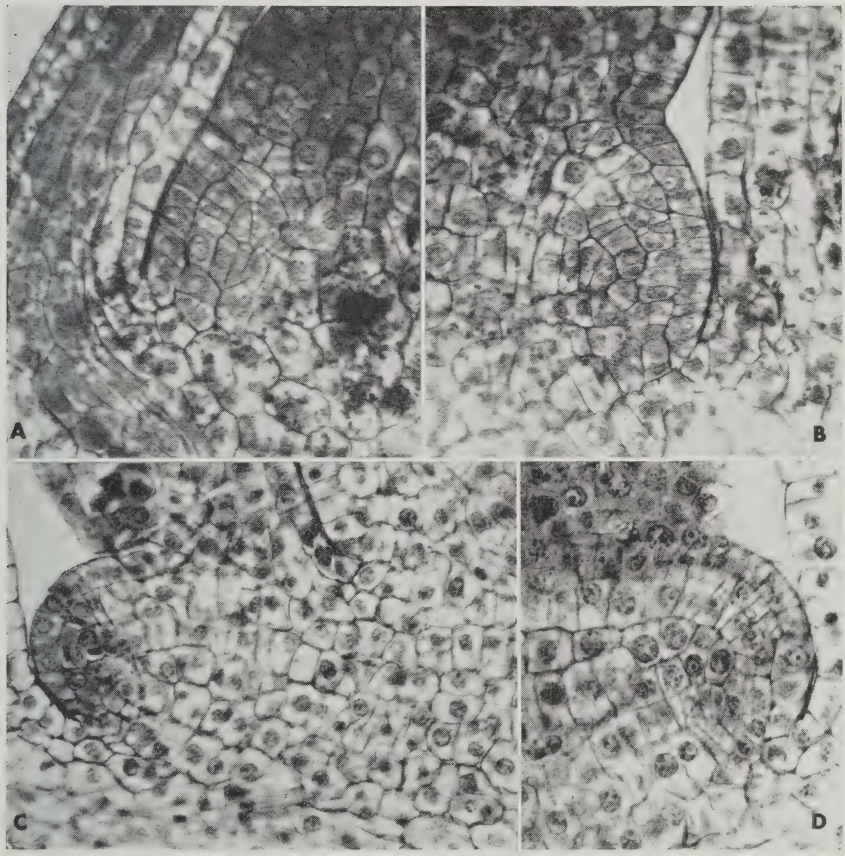


Initiation and early stages of the development of the ligule shown in the longitudinal sections through the primordia. (Fig. 8)

A. Initiation of the ligule begins by a periclinal cell division in one of the group of meristematic cells at the point where leaf blade and leaf sheath join. ×440.

B-D. Successive stages in the initiation and development of the ligule. ×440.

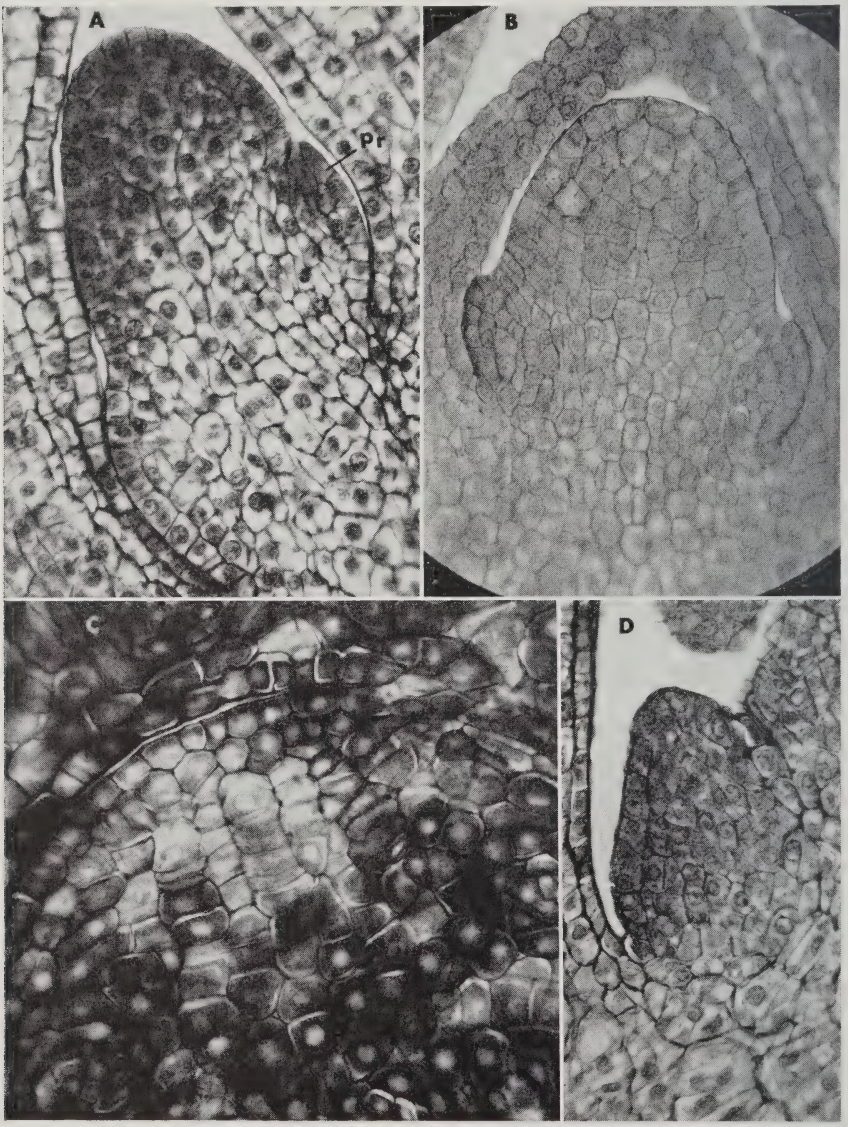
periclinal cell division in one or both of the central cells of the group (*Fig. 8: A, B*). Both anticlinal and periclinal cell divisions occur among the initiating cells, resulting in an elongated structure several cells long which projects upward parallel with the leaf blades (*Fig. 8: C, D*). The ligule may be several cells wide at the point of its insertion, narrowing to two cells at the tip. The initiation and development of the ligule resemble those of the stigmatic branch of the silk, which originates from a single epidermal cell (Weatherwax, 1917).



Initiation and development of tiller primordia. (Fig. 9)
A. A median longitudinal section through a tiller primordium. Initiation begins with periclinal divisions of the cells in the third layer of the shoot. ×440.
B-D. Median longitudinal sections of successively more advanced stages in the development of the tiller primordium. Radial files of cells are characteristic of the early stage of tiller development. B, ×440; C, ×300; D, ×430.

Axillary Shoots and Tillers

Unlike leaves, axillary-shoot primordia are initiated by periclinal divisions in the third cell layer of the shoot. Initiation of the axillary shoot is illustrated in *Figs. 9: A* and *10: C*. The observations made in



(Fig. 10. — See opposite page)

this study are in agreement with those of Sharman (1942). He stated that he had never found periclinal cell divisions in the outermost cell layer at the position of the tip of the tiller-bud primordium either in the early stage or during its emergence. Rarely are periclinal divisions found in the first cell layer (mantle) at the apex of the main shoot.

The tiller primordium begins to develop in the shoot at a point opposite and a little above the upper margin of the leaf. It is located on the circumference of the stem at the point where the margins of the subtending leaf meet. Since the margins of the preceding leaf do not quite meet, there is at this point on the stem a gap in which the tiller primordium is inserted. The tiller primordium develops in the internode above the subtending leaf. This can be seen in *Fig. 9: A* but more clearly in *9: C*, where the long files of cells extending centripetally from the tiller primordium lie above the upper margin of the preceding leaf and below the lower margin of the leaf above. This is the internode region of the stem.

Following the periclinal cell divisions which initiate the tiller primordium, many cell divisions occur in this area. Many oblique as well as anticlinal divisions occur, producing radial files of cells (*Fig. 9: B, D*). In the longitudinal sections (*Fig. 9: B, C, D*) and the cross-section (*Fig. 10: C*), the cells inside the stem and bordering the initiation point of the primordium are narrow rectangles, indicating an area of rapid cell division. In the apex of the shoot of the tiller primordium and behind the area of rapid cell division, the cells are larger. Cell division is more rapid on the basipetal side of the primordium, thus turning the axillary shoot upward approximately parallel with the main axis (*Fig. 10: D*). At the same time anticlinal cell divisions occur in the first cell layer, keeping pace with the growth of the apex of the axillary shoot.

The zonal organization of the shoot is forecast from the beginning of the initiation of the tiller primordium. The first periclinal cell di-

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Tiller development. **(Fig. 10)**

A. A longitudinal tangential section of a tiller primordium. The primordium of the prophyll (pr) is at the upper right side of the tiller. ×300.

B. A median longitudinal section of a tiller primordium at right angles to the plane of the leaves. A leaf primordium at the base of the shoot is the last one initiated. The shoot apex resembles that of the main axis in the vegetative stage. This type of shoot develops into the ear. ×270.

C. A transection through the tiller primordium of maize embryo. Files of periclinally dividing cells characteristic of early stages of development of tiller primordia are present. ×735.

D. A longitudinal section through a tiller primordium before the initiation of the prophyll. ×290.

visions (*Fig. 9: A*) are in the third cell layer and are the first cells of the subapical meristem of the axillary shoot.

The first cell layer of the parent axis can be seen as the first cell layer, the mantle, of the shoot apex of the axillary shoot. It is that area of the stem, just above the subtending leaf, where the narrow anticlinally dividing cells are grouped opposite the point of initiation of the tiller primordium (*Fig. 9: A*). The mantle and the subapical meristem are shown in *Fig. 9: B*. In the *D* section of this illustration, the central meristem is represented by the group of narrow cells immediately to the left of the subapical cells. The cells in the second layer of the tiller primordium are in the position that the peripheral meristem occupies in the more mature shoot. As the axillary shoot increases in size, the meristematic zones characteristic of a mature shoot become more clearly defined (*Fig. 10: B*). The shoot apexes of the lateral shoots of the main axis and, as will be shown later, the floral shoots, repeat the developmental cycle of the shoot of the main axis. The stages of development in the tiller are not concurrent with those of the main axis.

The prophyll. A prophyll is the first foliar member to form on the axillary shoot. It is located between the axillary shoot and the main axis (*Fig. 10: A-pr*), with the ventral side next to the main axis, and is initiated in the same manner as a leaf. It is a two-keeled structure, having two principal vascular bundles, one in each keel. Regarding the nature of the prophyll, Arber (1934) states: "Although the prophyll has two principal bundles its symmetry is not really duplex, for one of the bundles is, as a rule, earlier in development and larger than the other." This author also points out that the axillary bud of the prophyll, when present, lies opposite the larger bundle. However, Collins (1924) was of the opinion that the prophyll is composed of two leaves that have fused at the margin. He stated that in certain Mexican maize types, in teosinte (*Euchlaena mexicana*), and in F_2 progeny of certain teosinte-maize crosses, two secondary branches were found in the axil of the prophyll. He supported his viewpoint with a photograph of an ear and two large secondary ears.

The observations made in this study support those of Arber (1934) as to the asymmetry of the prophyll, the difference in the size of the two principal vascular bundles, and the position of the axillary bud of the prophyll. It was also noted that the initiation of the first foliage leaf occurs on the side of the axis opposite the large vascular bundle of the prophyll, and that the principal vascular bundle of the first foliage leaf is also opposite the major bundle of the prophyll.

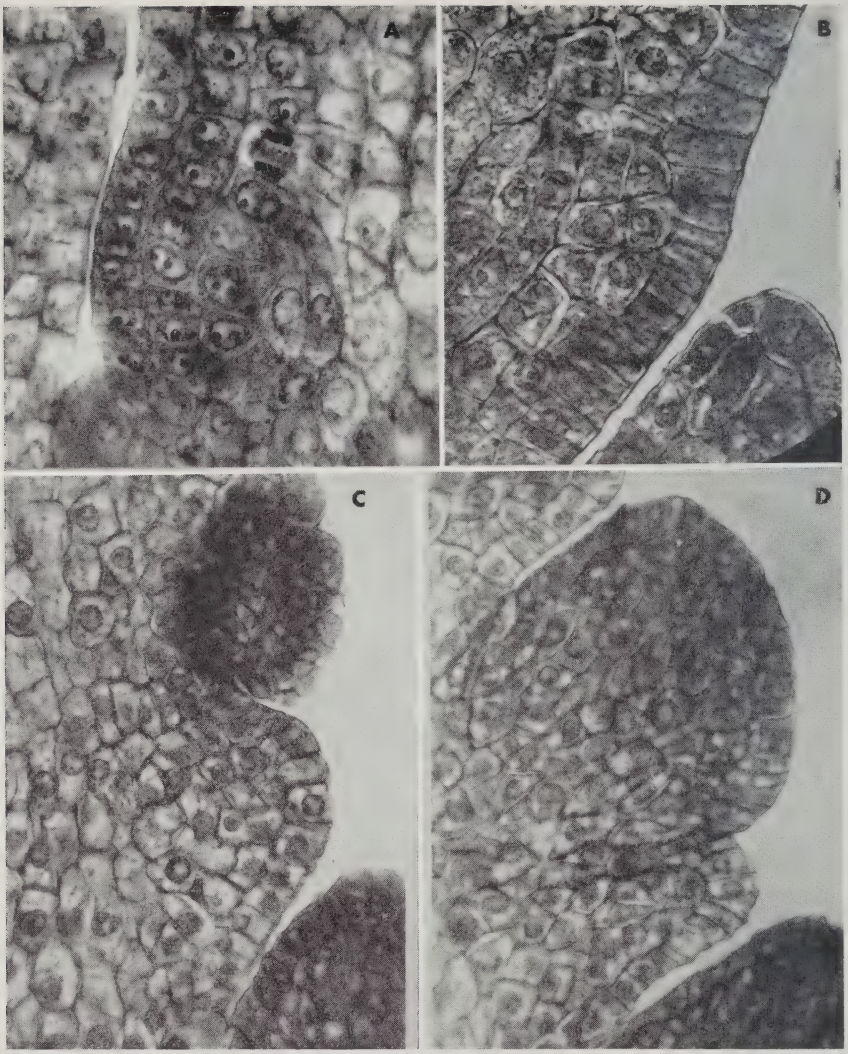
The Floral Shoot

Floral initiation begins in either the tassel or the ear shoot with the initiation of branch primordia at the base of the elongated axis. This occurs when the shoot apex in the transitional stage becomes about twice as long as its diameter. The first branch primordia form just above the insertion of the upper margin of the last leaf primordium (*Fig. 11: A*). Differentiation of the primordia proceeds acropetally. The number of the branch primordia around the circumference of the shoot apex of the ear or tassel and their arrangement on the axis vary with the kernel-row number of the ear.

Initiation of branch primordia, the long branches of the tassel and the spikelet-forming branches of the tassel and ear, as previously stated, is preceded by the development of a ridge beneath the primordium (*Fig. 1: D, E*). This subtending ridge is found in the inflorescence of many cereal and forage grasses. The prominence of the ridge in the mature tassel varies in the different maize varieties and types; but it can always be found in the earliest stages of tassel development. In the ear the ridge is quite prominent, and the lateral margins develop into projections which Arber (1934) called "rachilla flaps." Cutler and Cutler (1948) and Lenz (1948) called them rachis-flaps, which is the term used in this publication.

Cutler and Cutler (1948) said: "The rachis-flap resembles the auricle of the leaf in shape and this resemblance is heightened by the presence below it of the pulvinous notch, a small notch often formed at the margins of a leaf, bract or glume at the point of its union with the node." Lenz (1948) pointed out that the rachis-flaps in cross-section show conspicuous differences in size and shape among various varieties of maize. He shows outline drawings of cross-sections of the rachis-flap of sixteen varieties of maize.

Initiation of the ridge subtending the branch primordia of the ear and tassel begins with periclinal cell divisions in the second cell layer of the shoot and later in the third cell layer (*Fig. 11: B*). Cross-sections through the region of the developing ridge show that periclinal cell divisions extend throughout the area of the stem beneath the branch primordium and involve many cells. The ridge grows by periclinal cell divisions in the second, third, and deeper layers of the shoot, resulting in the projection of the ridge from the surface of the shoot (*Fig. 11: C, D*). Anticlinal cell divisions occur in the epidermal (first) cell layer to accommodate it to the growth of the ridge. At the lateral extremities of the ridge primordium, periclinal cell divisions in the shoot extend downward parallel with the long axis of the shoot to



Branch primordium and ridge subtending the branches in the ear. (Fig. 11)

A. A longitudinal section through a branch primordium of the tassel. The transitional stage terminates at this point and the reproductive stage has begun. ×730.

B. Initiation of the ridge subtending a branch primordium begins with periclinal cell divisions in the second cell layer of the shoot. ×730.

C. A longitudinal section through a ridge subtending a spikelet at the lateral margin of the insertion of the spikelet. This section includes a section of the rachis-flap. ×460.

D. A longitudinal section of the ridge subtending the spikelet primordium near the midpoint of the spikelet insertion. ×460.

form the rachis-flap (*Fig. 2: E-r* and *Fig. 11: C*). Directly beneath the spikelet the ridge is narrow at the apex, becoming wider toward the interior of the stem (*Fig. 11: D*).

The position of the ridge suggests that it may be a very much suppressed leaf. However, the initiation of the ridge differs from that of a leaf primordium in that there are no periclinal divisions in the first cell layer of the shoot, as there are in the initiation of the leaf. If it is homologous with a leaf, it has been suppressed to the point that no remnant of the leaf remains and instead excessive development of the nodal tissue occurs. A study of cleared sections of the axis of the ear shows that the vascular bundles extend parallel with the long axis of the ear through the rachis-flaps and transversally through the ridge beneath the spikelet. No bundles are found that might be interpreted as belonging to a leaf. In view of the evidence it seems that the best interpretation is to consider the ridge subtending the branch primordia as consisting of extensions of the nodal tissue. The rachis-flap may be an extension of the subtending ridge or a special development of the rachis(cob).

Spikelet-forming branches. The spikelet-forming branch primordia and the primordia of the long branches of the tassel originate at a point slightly above, acropetally, the subtending ridge. Both primordia are initiated by periclinal cell divisions in the third cell layer of the shoot in the same manner as shoots formed in the axils of foliage leaves. This can be seen by comparing *Fig. 11: A*, which shows the primordium of a long branch of a tassel, with *Fig. 9: A*, which shows the primordium of a tiller. It is difficult to determine from serial sections whether the branch primordium starts from the periclinal division of a single cell or of a group of cells. When the primordium can be identified with certainty, several cells can be found that have divided periclinally and they form a spherical group. Many anticlinal cell divisions occur in the first and second cell layers of the shoot at the point of emergence of the apex of the branch primordium. Many cell divisions occur in the shoot above and below the point of initiation of the primordium as well as in the interior of the stem behind the point of initiation, producing radial files of cells. Rapid cell division on the basipetal side of the primordium results in its protruding from the surface of the shoot and extending acropetally parallel with the main axis.

It has been pointed out (*Fig. 2: A, B, C*) that at first the spikelet-forming branch primordia appear to be single and that later an unequal division occurs, resulting in two spikelet primordia. Serial cross-sections through these primordia show that before the primor-

dium emerges from the surface of the shoot two growth centers are present. These are the spikelet primordia. A large cell, a periclinally dividing cell, or a group of periclinally dividing cells can be found on either side of the center of the spikelet-forming branch primordium. Cell divisions in all planes produce a spherically shaped group of cells which is the subapical meristems of the spikelet primordia. The two spikelet primordia are not initiated in the same horizontal plane. The cells of the smaller spikelet primordium (sessile spikelet) are slightly lower, basipetally, than those of the larger spikelet primordium (pedicellate spikelet).

From this and previous studies (Bonnett, 1940, 1948) it seems clear that the spikelet-forming branches of the tassel and ear of maize are branches of the first order. The spikelet primordia are branches of the second order and, as will be shown later, the flower primordia are branches of the third order.

Branches of the first order, the spikelet-forming branches, give rise to two branches of the second order, the spikelet primordia, each of which gives rise to two branches of the third order, the upper and lower flowers. The branches in each of the orders arise acropetally and have an alternate arrangement upon each of the parent axes. This is consistent with the order of differentiation and arrangement of the branches on the main axis. However, the homology is not complete. The homologue of the prophyll is lacking for the spikelets, which arise from the spikelet-forming branch. No remnant of the axis of the spikelet-forming branch is found between the two spikelets. Neither is there a remnant of the rachilla found between the two flowers although Arber (1934) reported finding evidence for one. Weatherwax (1925) has also shown a prolongation of the rachilla in multiflowered spikelets of a dwarf type of maize, but in another illustration the topmost flower terminates the rachilla. In this investigation it was found that the primordium of the pedicellate spikelet seems to terminate the axis of the spikelet-forming branch, and the upper flower of a two-flowered spikelet seems to terminate the rachilla.

That the spikelet-forming branch, although very much reduced, is a branch of the first order is borne out by observations that have been made on mature inflorescences. A short spikelet-forming branch from which the spikelets arise can be found in the mature tassels of many maize varieties while in other varieties the branch is reduced to the point that the sessile spikelet seems to be attached directly to the main axis. Occasionally in the tassel of fasciated types of maize, a group of three spikelets can be found arising from the same branch. Such a

group shows acropetal succession and alternate arrangement on the axis. Brieger (1945) found more than two spikelets arising from the spikelet-forming branch. They appeared to have risen acropetally and to be alternately placed upon the branch.

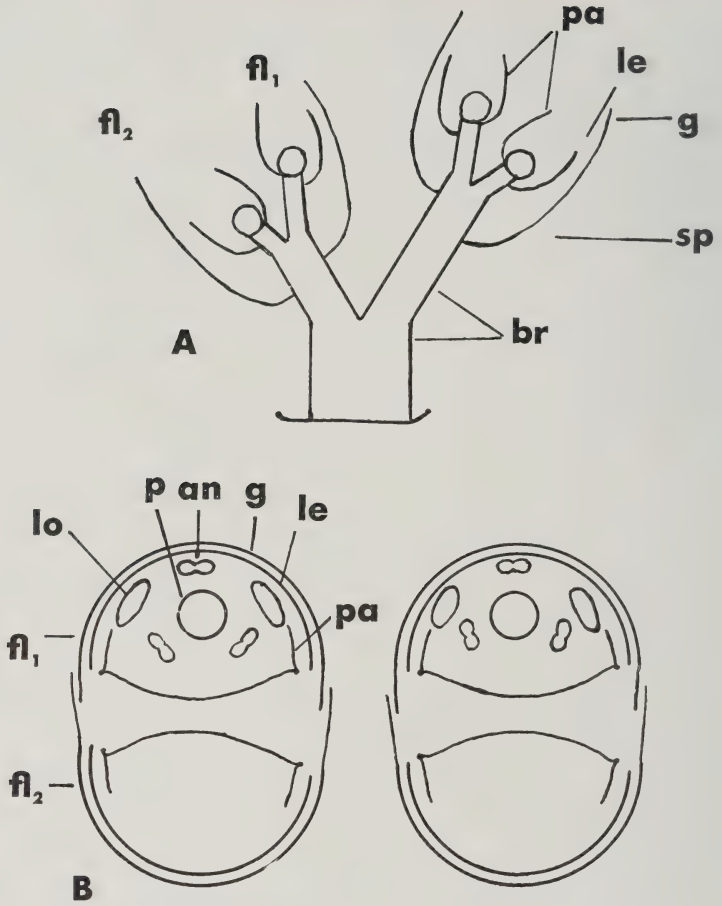
In the mature ear the spikelet-forming branch primordium is suppressed to the point that the spikelets appear to originate from the main axis. However, the earliest stages of development of the ear appear no different from the same stages of the tassel.

The spikelet. The spikelets and flowers of both the ear and tassel are modified shoots. They produce leaflike structures, empty (sterile) glumes, and flowering glumes. In the tassel the empty glumes are thin and long enough to enclose completely the flowers, but in the ear they are thick and horny and only partly enclose the flowers. The empty glumes arise from the lateral branches of the spikelet-forming branch. The lemma and palea are the flowering glumes since they enclose the flower parts. The palea has two keels like the prophyll with which it is homologous. The arrangement of the glumes on the axes and their relationship to each other in the spikelet are shown in the diagrammatic drawings in *Fig. 12*. The glumes, lemmas, and paleas are formed acropetally from the shoot apex, and they are arranged alternately upon their axes.

The node enlarges where the glumes, lemmas, and paleas are inserted into the axis. At the earliest stage of development, a protuberance can be seen on the axis beneath the abaxial empty glume and in certain specimens beneath the adaxial glume. The internodes between the glumes remain short.

The initiation of glumes, lemmas, and paleas is like that of foliage leaves, so these parts are considered modified leaves. Periclinal cell divisions occur in the first and second cell layers of the shoot. Initiation begins on one side of the shoot and proceeds in both directions about halfway around the shoot. Elongation, marginal development, and other developmental events are the same as for foliage leaves. The initiation of glumes and lemma is shown in *Fig. 13*. There is no difference in the initiation of the palea, glumes, or lemma (*Fig. 14: B-pa*).

Glumes, lemmas, and paleas have been interpreted as the sheaths of the leaves. Since glumes are like leaves in their initiation and early stage of development, and since the blade of the foliage leaf is the first part of a leaf to develop, it seems inconsistent to interpret the glume as a leaf sheath. A better interpretation would be to consider it the modified tip of the blade of the leaf.

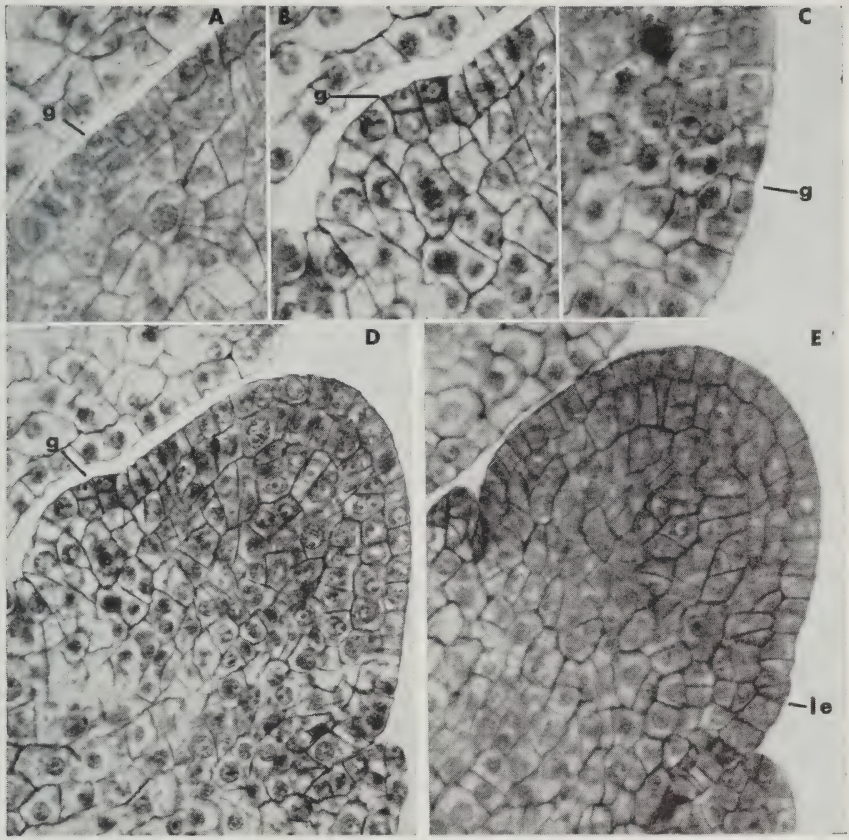


Arrangement of spikelets and their parts in longitudinal section and transection. (Fig. 12)

A. A pair of spikelets each containing a pair of flowers. The branching and the position of the glumes, lemmas, and paleas, and the reproductive organs on the branches are presented diagrammatically. The orientation of the spikelets with respect to each other is not correct. The circles represent the stamen and pistil.

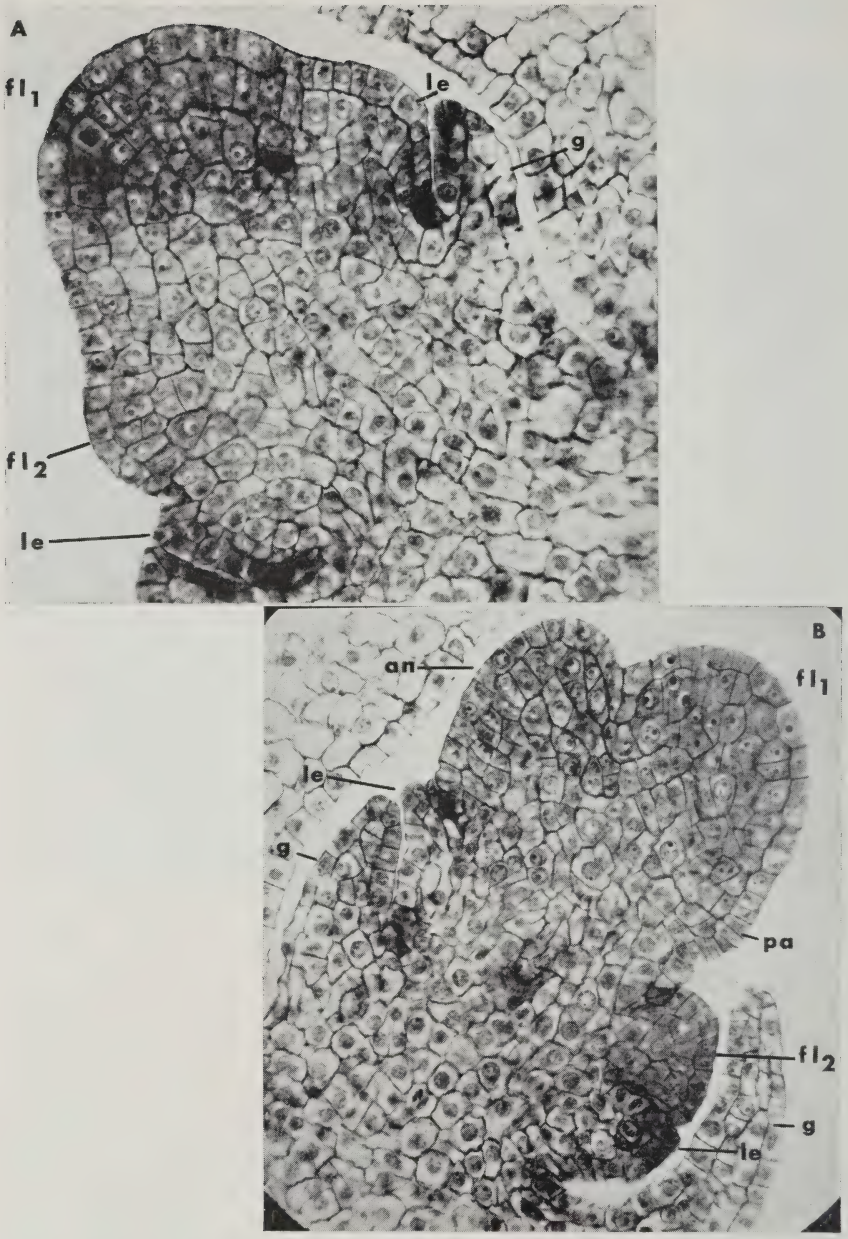
B. Transections of a pair of spikelets oriented in the position that they have to each other on the ear or tassel. The upper flowers of the spikelet are on the adaxial side of the spikelet. The lower flowers are without pistil or stamen. They represent the abortive flower in the ear of most maize types.

(an = stamen; br = branches; fl_1 = upper flower; fl_2 = lower flower; g = glume; le = lemma; lo = lodicule; p = pistil; pa = palea; sp = spikelet)



Initiation of the glumes and lemma. (Fig. 13)
A, B, D. Adaxial glume of the spikelet. ×660.
C. Abaxial glume. ×440.
E. Lemma of the lower flower. ×440.
(g = glume; le = lemma)

The flower. A maize flower is an axillary shoot. It arises from an axis, the rachilla, in the axil of the lemma. The lower flower is initiated by periclinal cell divisions in the third cell layer of the shoot above the lemma (*Fig. 14: A-fl*$_2$ *and le*). The development of the lower flower is similar to that of a lateral axillary shoot. The upper flower terminates the axis, with the lemma differentiating on the adaxial side (*B-le*) and the palea on the abaxial side of the axis (*B-pa*). In *B* the palea has not yet been initiated. A stamen primor-



Early stages in the development of the spikelet. (Fig. 14)

A. A median longitudinal section of a pistillate spikelet. The lower flower is a lateral shoot which is initiated by periclinal cell divisions in the third cell layer of the shoot. Primordia of the glumes and lemmas are shown. ×440.

B. A tangential longitudinal section of a pistillate spikelet. Various parts of the upper and lower flowers are shown. ×340.

(an = anther; fl_1 = upper flower; fl_2 = lower flower; g = glume; le = lemma; pa = palea)

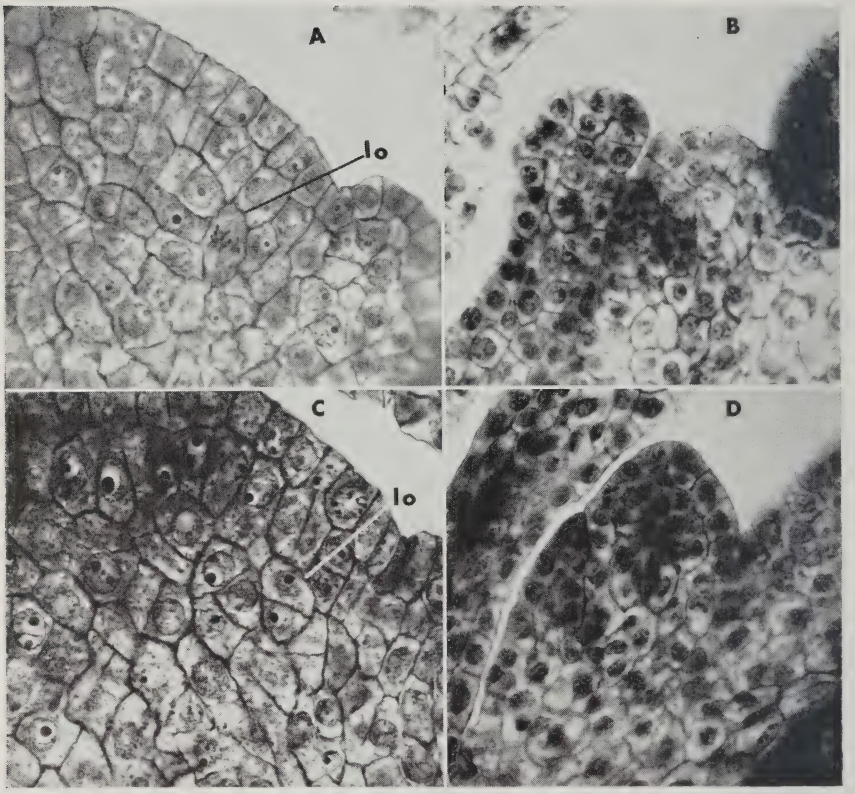
dium is shown at the upper portion of *B-an*. As stated before, the lower flower in the spikelet of the ear of most maize types is nonfunctional.

A maize flower is in some respects similar to other axillary shoots, but in other ways different. It is like other shoots in that it arises in the axial of a leaf, the lemma, and it has a prophyll, the palea. It differs in that it gives rise to special parts, two lodicules, three stamens, and a pistil. The two lodicules of the maize flower represent two of three members of a perianth whorl. They are located on the adaxial side of the flower shoot opposite the lateral margins of the lemma. The third member of the whorl, which would be located on the adaxial side of the shoot opposite to the middle of the lemma, is absent. The lodicules, transversally broad at the base, are long pointed structures which become turgid at anthesis and serve to force the glumes apart so that the anthers can be easily exerted from the glumes. The lodicules are present in the flowers of both the tassel and ear, but they are small and nonfunctional in the flowers of the ear. The three stamens form a whorl inside the whorl of lodicules. Two of the stamens are placed on the adaxial side of the shoot opposite the two keels of the palea. The third stamen is on the abaxial side of the shoot at a point midway between the two lodicules.

The stamens in the flowers of an ear are initiated, but they do not complete their development (*Fig. 3: C-an*). Since the upper flower develops a functional pistil, the degree of development attained by its stamens is greater than that of the abortive lower flower.

Lodicules and stamens are branchlike parts. Both are initiated by periclinal cell divisions in the third cell layer of the floral shoot, and no periclinal cell divisions occur in the first cell layer during their initiation. Lodicules are initiated at a point in the shoot just above the insertion of the lemma (*Fig. 15: A, C-lo*). As the lodicule primordia develop, they have the appearance of the primordia of a shoot (*Fig. 15: B, D*). The initiation of a stamen primordium is shown in *Fig. 16: A, B, C*. Periclinal cell divisions have occurred in the third and deeper cell layers. No periclinal cell divisions are found in the first cell layer over the point of initiation of the stamen primordium. More advanced stages of development of a stamen are shown in *Fig. 16: D, E, F*. Satina and Blakeslee (1941) observed that the stamen of *Datura stramonium* is initiated by periclinal cell divisions in the third cell layer of the shoot. That the stamens are branchlike structures is in accord with the interpretation of Wilson (1942).

The pistil of maize consists of three fused carpels, in which is one ovule with two integuments. The two carpels on the side of the shoot



Lodicule initiation and early stages of development. (Fig. 15)

A, C. Longitudinal sections through flowers showing the beginning of lodicule initiation. A single large cell which is dividing periclinally is shown on the right side at the base of the shoot in each photograph. ×660.

B, D. Longitudinal sections through lodicule primordia. They are shootlike in appearance. ×440.

(lo = lodicule primordium)

Longitudinal sections showing initiation and development of stamen. (Fig. 16)

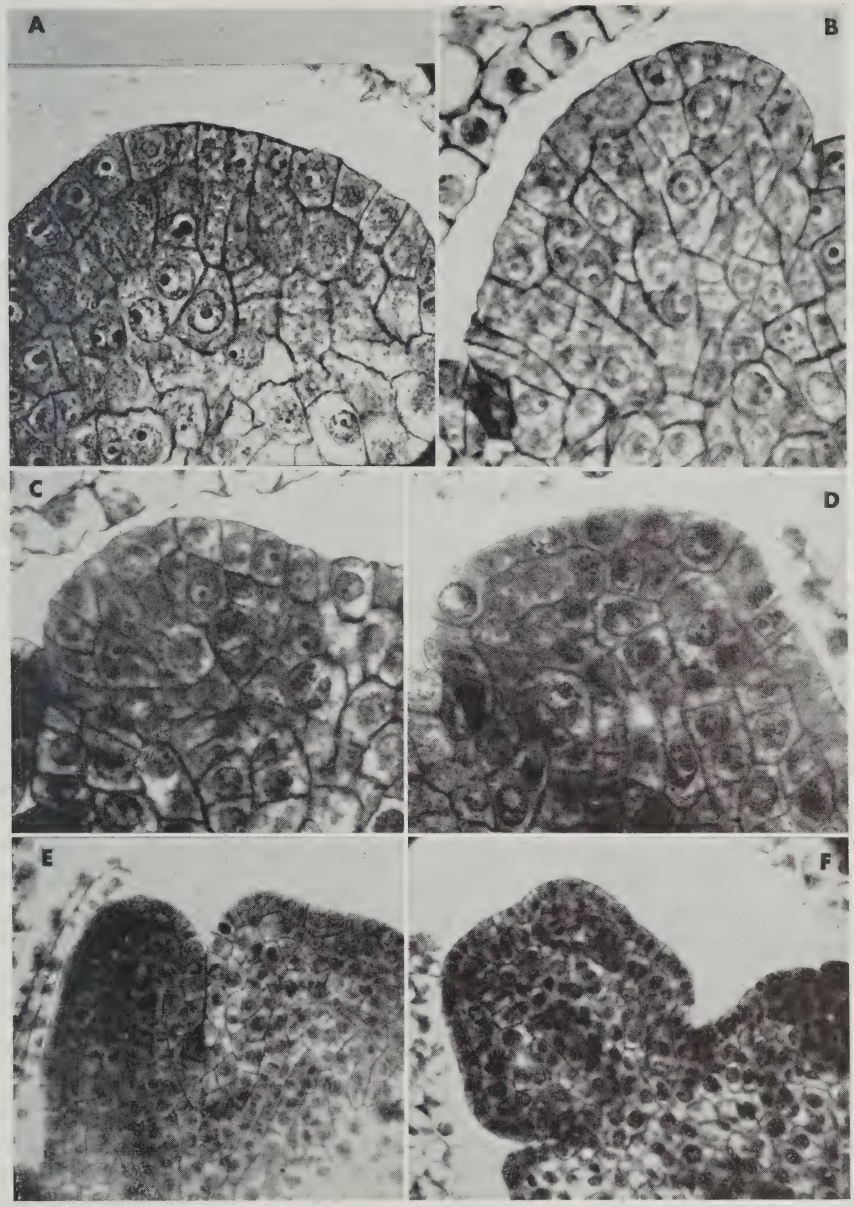
A. Longitudinal section through the flower at the point of initiation of the stamen. Stamen initiation begins with periclinal cell divisions in the third cell layer of the shoot. Anticlinal cell divisions are present in the first cell layer at the point of stamen initiation. ×660.

B, C. Early stages in the development of the stamen. The primordia resemble shoots. B, ×625; C, ×625.

D. The stamen primordium is flattened at the tip preceding the formation of the locules of the anther. ×660.

E. Elongation of the stamen primordium. ×275.

F. Formation of the locules of the anther has occurred. ×275.

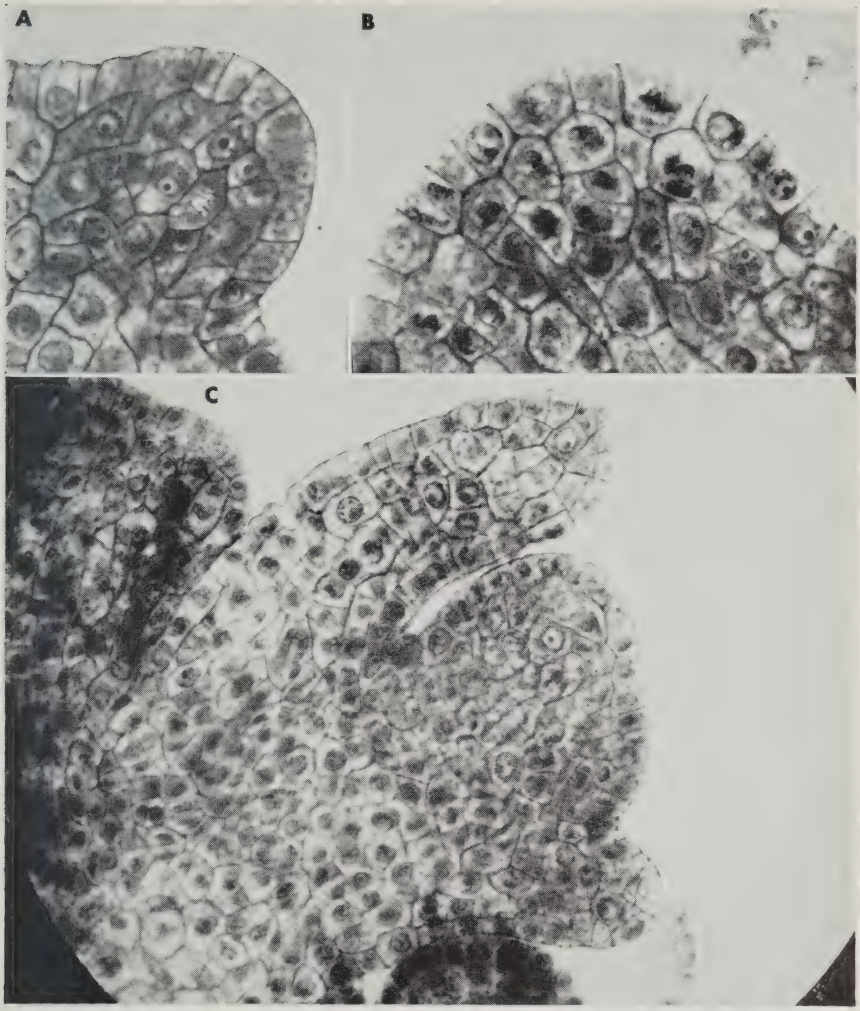


(Fig. 16. — See opposite page)

next to the lemma elongate, producing two styles fused along their inner margins except at the very tip where the styles are divided to produce a biparted tip. The third carpel is located on the side of the shoot opposite the palea. Two integuments arise beneath the apex of the shoot. The ovule proper is formed from the apex of the floral shoot.

Carpels are initiated by periclinal cell divisions in the first and second cell layers at the apex of the shoot shown in *Fig. 17: B*; the shoot apex before the initiation of the carpels is shown in *A*. Differentiation of the carpel extends laterally around the shoot, forming a collarlike structure (*Fig. 3: C, D, E* and lower flower *H*). The initiation and development of the carpels resemble the initiation and development of a leaf, and therefore carpels are considered to be leaflike structures. *Figure 17: C* is a longitudinal section through a pistil. The carpels have elongated so as partly to enclose the ovule. *Fig. 17* is at a stage similar to *Fig. 3: G*. The two carpels on the side of the shoot apex next to the lemma elongate to produce two styles, fused along their inner margins except at the tip (*Fig. 3: F, G, H*). Extending throughout the length of each style is a vascular bundle which connects with the vascular bundles leading to the spikelet. A strand of stigmatoid tissue (Esau, 1953), through which the pollen tube grows, is located on the side toward the fused margin of the style and accompanies the vascular strand of the style. As the carpels grow they enclose the ovule, except for the stylar canal where the carpels join. The carpels form the ovary wall which encloses the ovule with its integuments. The tricarpellate nature of the pistil is not indicated from its external appearance during its initiation (*Fig. 3: C, D, E*). It appears to be a unit. Keisselbach (1949) has an illustration showing a pistil of maize with the third carpel well developed, producing a tristylar silk containing three vascular bundles. The tricarpellate nature of the maize pistil must be arrived at from evidence other than that obtained from a study of its initiation and early stage of development.

The maize pistil has two integuments which, like leaves, are initiated by periclinal cell divisions in the first and second cell layers of the shoot (*Fig. 18: C, D*). The outer integument is initiated first at a point just above the insertion of the carpel, and its differentiation like that of a leaf, extends around the ovule (*A*). It remains short, is several cells wide at the base, but narrows to two or three cells at the tip. The outer integument only partly encloses the ovule. *B* is a longitudinal section through an ovule, showing the outer integument. The inner integument is initiated at a point on the shoot above the outer integument. The inner integument, two or three cells thick, covers the ovule

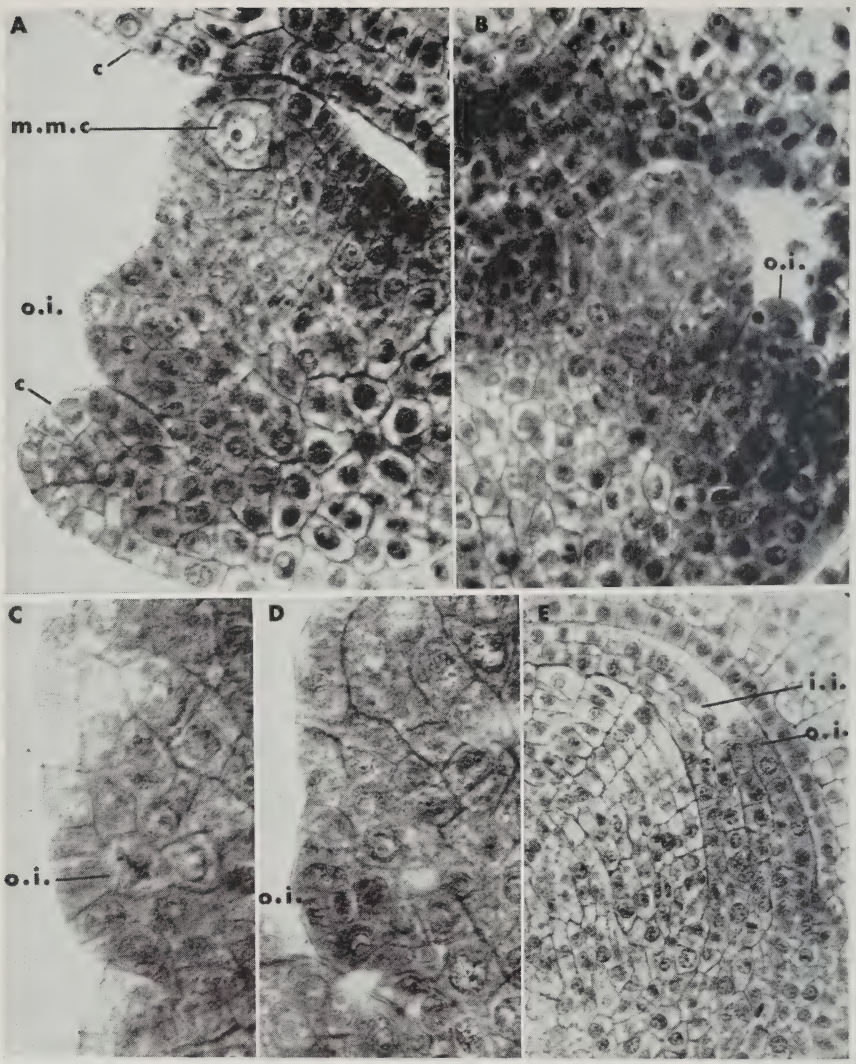


Carpel initiation and development. (Fig. 17)

A. A median longitudinal section of the floral shoot preceding the initiation of the carpel. ×665.

B. Initiation of the carpel begins with periclinal cell divisions in the first and second cell layers of the shoot (upper right). ×665.

C. Longitudinal section of a pistil showing the carpels and ovule. ×390.



Initiation and development of the integuments of the ovary. **(Fig. 18)**

A. Median longitudinal section of a pistil showing the lower carpel, outer integument, and the megasport mother cell. ×440.

B. Outer integument covering a portion of the ovule. ×440.

C, D. Periclinal cell divisions which initiate an integument are shown in the first and in the second cell layers of the shoot. ×735.

E. A tangential longitudinal section of an ovule to show the integuments. The inner integument completely covers the ovule. The outer integument is short. Enlarged.

(c = carpel; o.i. = outer integument; i.i. = inner integument; m.m.c = megaspore mother cell)

except for the micropyle (*Fig. 18: E-i.i.*). The micropyle opens at a point opposite the embryo sac and is oriented toward the palea (adaxial). An integument can be seen as a ridge on the ovule in *Fig. 3: H.*

The ovule is a prolongation of the floral axis, terminating the axis (*Fig. 3: G, H* and *Fig. 18: B*). More rapid growth occurs on the side next to the rachilla (adaxial), turning the ovule to a position at right angles to its former position, thus forming a campylotropous type of ovule. The megaspore mother cell develops in the second cell layer directly beneath the shoot apex (*Fig. 18: A*).

The sequence of development of the spikelets and their parts may be summarized as follows. A spikelet-forming branch primordium gives rise to the sessile spikelet, then to the pedicellate spikelet. The sequence of development of a spikelet and its parts is: abaxial glume, adaxial glume, lemma of the lower flower, primordium of the lower flower, lemma of the upper flower, anther opposite the lemma of the upper flower, and palea of the upper flower. Within a functional flower, the initiation of the lodicules follows the formation of the palea, then the stamens opposite the palea are initiated. For the pistil the order is: the carpels, the outer integument, and the inner integument of the ovary. The palea of the lower flower develops when the flower attains sufficient size, which is after the stamens of the upper flower have differentiated.

DISCUSSION

Repetition in the kinds of organs and the sequence of their development is clearly demonstrated in the ontogeny of the maize plant. The main shoot gives rise to two kinds of lateral organs: leaves and leaflike parts, and shoots and shootlike parts. All lateral organs arise from the parent axis in acropetal succession. The leaf or leaflike part is initiated first and its shoot and shootlike part, second. Each organ of the same type is initiated in the same way — from the same cell layer or layers of the parent shoot — and follows a similar pattern of development in the early stage of development. Differences in adult parts of the same type result from differences in the development of the parts following their initiation.

The primordia of all plant parts, in their initiation, have one thing in common: all are initiated by a periclinal cell division or divisions in one or more of the surface cell layers of the shoot. Periclinal cell division is the mechanism by which lateral organs and protrusions emerge from a shoot or other plant part. Following initiation, not one

but many cell divisions occur in the same plane and so provide for elongation. Many such cell divisions in the same plane can be found in any part of the plant where rapid growth in length or width is taking place.

In maize the primordia of leaves and leaflike parts and shoots and shootlike parts originate in different cell layers of the shoot apex, and they follow different patterns of development. These differences are in accord with the essential differences in the function and the developmental patterns of the two types of parts. Leaves are determinate organs, without a self-perpetuating meristematic zone and, in the early stage, growth occurs at the apex and margins of the leaf. Marginal growth is maintained by periclinal cell divisions in the first and second cell layers of the primordium. The initiation of the leaf primordium by periclinal cell divisions in the first and second cell layers of the parent shoot is the beginning of the growth pattern characteristic of the leaf. Branches are indeterminate organs, having a permanent meristematic zone, the subapical meristem, from which the other meristematic zones, except the mantle, are derived. The first cell layer, the mantle, covering the shoot, accommodates itself to the growth of the shoot by anticlinal cell divisions, and rarely do periclinal cell divisions occur in it. The subapical meristem is maintained by periclinal cell divisions in the second cell layer at the shoot apex, although anticlinal cell divisions also occur in this region. The initiation of the shoot primordium begins with periclinal cell divisions in the third cell layer of the shoot, establishing the subapical meristematic zone of the shoot primordium. Later periclinal cell divisions occur in the second cell layer to maintain the subapical meristem. Cell divisions in other planes at the basipetal periphery of the subapical zone and periclinal divisions interior to the point of initiation are all consistent with the growth pattern of the shoot. The point of initiation and the growth patterns of the primordia of the two types of organs are consistent with the growth patterns of the adult organs and account for the differences in the point of their initiation and type of cell divisions.

The development of the tassel and ear of maize presents a number of contrasts. In the tassel long unilateral branches develop from the base of the inflorescence, and the spikelet-forming branches are confined to the long branches and the central axis. All the branches of the ear, except in ramosa, are spikelet-forming branches. The pairs of spikelets of the tassel are borne on pedicels of unequal lengths while in the ear the pedicels of the paired spikelets are short and apparently equal in length. Both flowers of the spikelet of the tassel are functional,

while in most maize types only one of the flowers of the spikelet in the ear is functional and the other aborts. In the flowers of both the ear and tassel, three stamens and a pistil are initiated, but the pistil aborts in the tassel and the stamens abort in the ear. The glumes, lemma, and palea of the flower of the tassel are long and thin, enclosing the stamens. In the ear the glumes, lemma, and palea of the flower are short, the glumes are thick and horny, and the lemma and palea are thin. Cuplike depressions develop in the axis of the ear in which the paired spikelets are inserted; the ridge beneath the spikelet is prominent, rachis-flaps develop on either side of the spikelet, and deep longitudinal grooves are formed between the rows of spikelets; the cob has a sclerenchymatous zone between the epidermis and the pith; none of these characteristics of the ear are present in the central axis of the tassel.

While there are marked contrasts in the characteristics of the tassel and ear of maize, there are also many correlations. Anderson (1944) has listed a number of them: (1) tassel internode condensation and an increase in kernel-row number in the ear; (2) tassel-branch length and ear length; (3) branch-length pattern of the tassel and ear shape; and (4) tertiary branches in the tassel and irregular rowing in the ear. Other correlations have been observed, such as similarity of the branch pattern in the tassel and ear of ramosa. In fasciated ear types, biparted and triparted central axes of the tassel are accompanied by a similar branching in the ear. Plants having extreme condensation in the internodes of the central axis of the tassel also have short, thick, blunt-tipped ears, with a high number of rows of kernels.

The homology of the ear and tassel has been questioned because of the many contrasting characteristics of the two inflorescences at maturity. In the earliest stages of their development, they are essentially alike in the kinds of parts they produce and in the initiation and development of the primordia of the parts. For example, the primordia of the long branches of the tassel and of the spikelet-forming branches are initiated in the same way and resemble each other in the early stage of their development. Suppression could account for the lack of elongation of the spikelet-forming branches. However, the differences between the mature tassel and ear, described above, do not appear to be the result of differences in the basic characteristics of the main axes or in the kinds of lateral organs arising from them. Any lack of similarity between the mature tassel and ear seems to result from differences in their differentiation patterns.

APPLICATION OF THE STUDY

A knowledge of the developmental morphology of the maize plant can help in many ways to solve problems of crop production and plant breeding. The problems of crop production have to do with the response of the plant to the external environment in such a way that the plant can produce a maximum of grain or forage or both. Plant breeding is concerned with the production of genotypes better able to cope with their external environment. Since the mature maize plant with a given genetic complex is the resultant of a definite developmental pattern modified by the external environment during its development, an understanding of the outcome must rest upon a thorough understanding of the variables concerned. Two sets of variables are the developmental pattern and the time sequence of this pattern.

In this study the maize plant has been shown to develop by definite stages. Although the stages merge together as a continuous process, certain definite developmental activities occur in each stage that do not occur in the others. These stages can be identified by the internal and external characteristics of the main shoot and the lateral shoots. Each more advanced stage of development terminates the major developmental processes that characterized the preceding stage. With this information at hand, Leng (1951) was able to determine the time-patterns in tassel development of certain maize inbreds and to compare the lengths of the two periods (1) from planting to tassel initiation and (2) from tassel initiation to anthesis in each inbred. Also certain conclusions were reached regarding how studies of the inheritance of earliness should be conducted.

By being able to identify the stages of development of the maize plant, a time schedule can be set up for the application of fertilizers, growth-regulating chemicals, and other treatments that would be correlated with definite stages of plant development. This should enable workers to interpret the effects of the treatments more accurately. Based on the work of Bonnett (1935, 1937), Andersen (1952, 1952) was able to identify and set up a series of developmental stages in the growth of barley and oat plants and to use this classification in a study of the effect of 2,4-D upon the plants when applied at different stages of development.

From a study of developmental morphology it is evident that genetic changes, however produced, must occur in those cells of a plant from which the reproductive cells are derived if the changes are to be transmitted to their progeny. The cells concerned vary with the plant's stage of development. For example, colchicine applied to the shoot of

a corn seedling for the purpose of producing a polyploid or a doubled monoploid must affect the subapical meristem. The subapical meristem is self-perpetuating and contributes cells to the peripheral meristem from which floral shoots originate. All or any part of the peripheral meristem derived from a polyploid cell or cells could produce polyploid reproductive parts and hence, correspondingly, reproductive cells of the same type. Later when the primordia of the stamen or pistil have differentiated, it is the cells that produce the reproductive cells that are concerned. Hence genetic changes not occurring in the cells from which the reproductive cells are derived are limited to the zygote in which they arise and are not transmitted to their progeny.

LITERATURE CITED

ABBE, E. C., and PHINNEY, B. O. (1951). The growth of the shoot apex in maize: external features. Amer. Jour. Bot. **38**, 737-744.

ABBE, E. C., PHINNEY, B. O., and BAER, D. F. (1951). The growth of the shoot apex in maize: internal features. Amer. Jour. Bot. **38**, 744-751.

ANDERSEN, SIGURD (1952). Methods for determining stages of development in barley and oats. Physiol. Plant. **5**, 199-210.

ANDERSEN, SIGURD (1952). Sensitivity to 2,4-D of barley and oats at different stages of development. Physiol. Plant. **5**, 321-333.

ANDERSON, EDGAR (1944). Homologies of the ear and tassel of *Zea mays*. Missouri Bot. Gard. Ann. **31**, 325-342.

ANDERSON, EDGAR, and BROWN, W. L. (1948). A morphological analysis of row number in maize. Missouri Bot. Gard. Ann. **35**, 323-336.

ARBER, AGNES (1934). The Gramineae: A study of cereal, bamboo, and grass. Cambridge University Press. 480p.

BONNETT, O. T. (1935). The development of the barley spike. Jour. Agr. Res. **51**, 451-457.

BONNETT, O. T. (1936). The development of the wheat spike. Jour. Agr. Res. **53**, 445-451.

BONNETT, O. T. (1937). The development of the oat panicle. Jour. Agr. Res. **54**, 927-931.

BONNETT, O. T. (1938). Hood and supernumerary spike development in barley. Jour. Agr. Res. **57**, 371-378.

BONNETT, O. T. (1940). The development of the staminate and pistillate inflorescences of sweet corn. Jour. Agr. Res. **60**, 25-38.

BONNETT, O. T. (1948). Ear and tassel development in maize. Missouri Bot. Gard. Ann. **35**, 269-287.

BRIEGER, F. G. (1945). Estudios sôbre a inflorescência de milho com referência especial aos problemas filogeneticos. Brágantia **5**, 659-716. (English summary.)

COLLINS, G. N. (1919). Structure of the maize ear as indicated in *Zea-Euchlaena* hybrids. Jour. Agr. Res. **17**, 127-135.

COLLINS, G. N. (1924). The phrophyllum of grasses. Bot. Gaz. **78**, 353-354.

CUTLER, H. C., and CUTLER, MARIAN C. (1948). Studies on the structure of the maize plant. Missouri Bot. Gard. Ann. **35**, 301-316.

ESAU, KATHARINE (1943). Ontogeny of the vascular bundle in *Zea mays*. Hilgardia **15**, 327-356.

ESAU, KATHARINE (1943). Origin and development of primary vascular tissues in seed plants. Bot. Rev. **9**, 125-206.

ESAU, KATHARINE (1953). Plant anatomy. John Wiley and Sons, Inc. New York. 735p.

EVANS, M. W., and GROVER, F. O. (1940). Developmental morphology of the growing point of the shoot and the inflorescence in grasses. Jour. Agr. Res. **61**, 481-520.

FOSTER, A. S. (1934). The use of tannic acid and iron chloride for staining cell walls in meristematic tissue. Stain Tech. **9**, 91-92.

FOSTER, A. S. (1936). Leaf differentiation in angiosperms. Bot. Rev. **2**, 349-372.

FOSTER, A. S. (1939). Problems of structure, growth, and evolution in the shoot apex of seed plants. Bot. Rev. **5**, 454-470.

FUJITA, T. (1939). Über die Organstellungen bei Maiskolben. Japanese Jour. Bot. **10**, 113-140.

HACKEL, EDWARD (1890). The true grasses. Henry Holt and Co.

HAMILTON, HELEN H. (1948). A developmental study of the apical meristem in four varieties of *Avena sativa* grown at two temperatures. Amer. Jour. Bot. **35**, 656-665.

HITCHCOCK, H. S. (1935). Manual of the grasses of the United States. U. S. Dept. of Agr. Misc. Pub. No. 200. 1040p.

HSÜ, JEN (1944). Structure and growth of the shoot apex of *Sinocalmus beecheyana* McClure. Amer. Jour. Bot. **31**, 404-411.

HUBBARD, J. E. (1951). Leaf patterns in mature embryos of corn. Master's thesis, University of Illinois.

JOHANSEN, D. A. (1940). Plant microtechnic. McGraw-Hill. 523p.

KEISSELBACH, T. A. (1949). The structure and reproduction of corn. Nebr. Agr. Exp. Sta. Res. Bul. 161.

KLIEM, FRITZ (1936). Vegetationspunkt und Blattanlage bei *Avena sativa*. Beitr. z. Biol. der Pflanz. **24**, 281-310.

LAUBENGAYER, R. A. (1948). The vascular anatomy of the four-rowed ear of corn. Missouri Bot. Gard. Ann. **35**, 337-340.

LAUBENGAYER, R. A. (1949). The vascular anatomy of the eight-rowed ear and tassel of Golden Bantam sweet corn. Amer. Jour. Bot. **36**, 236-244.

LENG, E. R. (1951). Time-relationships in tassel development of inbred and hybrid corn. Jour. Amer. Soc. Agron. **9**, 445-449.

LENZ, L. W. (1948). Comparative histology of the female inflorescence of *Zea mays* L. Missouri Bot. Gard. Ann. **35**, 353-376.

MANGLESDORF, P. C., and REEVES, G. R. (1939). The origin of Indian corn and its relatives. Tex. Agr. Exp. Sta. Bul. 574.

MANGLESDORF, P. C. (1945). The origin and nature of the ear of maize. Bot. Mus. Leafl. Harvard Univ. **12**, 33-75.

MILLER, E. C. (1919). Development of the pistillate spikelet and fertilization in *Zea mays* L. Jour. Agr. Res. **18**, 255-265.

MORLEY, THOMAS (1949). Staining of plant material cleared in NaOH. Stain Tech. **24**, 231-235.

NOGUCHI, YAKICHI (1929). Studien über die Entwicklung der Inflorzenzen und der Bluten bei Getreidepflanzen. Jour. Col. Agr. Imp. Univ. Tokyo. **10**, 247-303.

PERCIVAL, JOHN (1929). The wheat plant: a monograph. Duckworth and Co. London. 463p.

POPHAM, R. A., JOHNSON, T. J., and CHAN, A. P. (1948). Safranin and analin blue with Delafield's hematoxlin for staining cell walls in shoot apexes. Stain Tech. **23**, 185-190.

POPHAM, R. A. (1951). Principal types of vegetative shoot apex organization in vascular plants. Ohio Jour. Sci. **51**, 249-270.

PRAT, HENRI (1948). General features of the epidermis in *Zea mays*. Missouri Bot. Gard. Ann. **35**, 341-351.

RANDOLPH, L. F. (1936). Developmental morphology of the caryopsis in maize. Jour. Agr. Res. **53**, 881-916.

REEVES, R. G. (1950). Morphology of the ear and tassel of maize. Amer. Jour. Bot. **37**, 697-704.

RÖSLER, PAUL (1928). Histologische Studien am Vegetationspunkt von *Triticum vulgare*. Planta **5**, 28-69.

SATINA, S., and BLAKESLEE, A. F. (1941). Periclinal chimeras in *Datura stramonium* in relation to development of leaf and flower.. Amer. Jour. Bot. **28**, 862-871.

SHARMAN, B. C. (1941). Development of the ligule in *Zea mays L.* Nature **147**, 641-642.

SHARMAN, B. C. (1942). Developmental anatomy of the shoot of *Zea mays* L. Ann. Bot. **6** (n.s.), 245-282.

SHARMAN, B. C. (1943). Tannic acid and iron alum with safranin and Orange G in studies of the shoot apex. Stain Tech. **18**, 105-111.

SHARMAN, B. C. (1945). Leaf and bud initiation in the *Gramineae*. Bot. Gaz. **106**, 269-289.

STANT, MARGARET Y. (1952). The shoot apex of some monocotyledons. Ann. Bot. **16** (n.s.), 15-128.

WEBER, HANS (1938). Gramineen-Studien. I. Über das Verhalten des Gramineen-Vegetations Kegels beim Übergang zur Inflorszenbildung. Planta **28**, 275-289.

WEBER, HANS (1939). Gramineen-Studien. II. Über Entwicklungs-gechichte und Symmetrie einiger Grasinfloreszenzen. Planta **29**, 426-449.

WEATHERWAX, PAUL (1916). Morphology of the flowers of *Zea mays*. Torrey Bot. Club Bul. 43, 127-144.

WEATHERWAX, PAUL (1917). The development of the spikelets of *Zea mays*. Torrey Bot. Club Bul. 44, 483-496.

WEATHERWAX, PAUL (1923). The story of the maize plant. Univ. of Chicago Press. Chicago, Ill. 247p.

WEATHERWAX, PAUL (1925). Anomalies in maize and its relatives — II. Many-flowered spikelets in maize. Torrey Bot. Club Bul. 52, 87-92.

WILSON, C. L. (1942). The telome theory and the origin of stamen. Amer. Jour. Bot. **29**, 759-764.

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